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Taphonomy of Verreaux's Eagle (*Aquila verreauxii)* prey accumulations from the Cape Floral Region, South Africa: implications for archaeological interpretations

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ABSTRACT

We conducted a taphonomic analysis of modern prey accumulations of Verreaux's Eagle (VE; *Aquila verreauxii)* from the Cape Floral Region of South Africa. VE nest in or around cliffs and rocky outcrops, places that also attract other bone accumulators, including humans. Therefore, it is necessary to characterize the signatures of VE bone accumulation with as much precision as possible in order to differentiate between the prey remains of other bone accumulators, especially in relation to fossil assemblages that originate in and around cliffs, rock shelters, and caves. Towards this end, we describe the taxonomic composition, skeletal-part representation, bone breakage patterns, and bone surface modifications of mammal bones as well as the range of variability within those signatures. Based on the frequency of bone modifications we determine that VE modify the bones of their prey more often than do other eagle species. We suggest that taphonomic patterns derived from predation by other eagle taxa are not the most appropriate means to identify VE predation in faunal assemblages. In addition, we conclude that there is patterned variability in the ways that VE accumulate and modify the bones of their prey. There are two distinct skeletal-parts preservation, bone breakage, and bone surface modification patterns among the prey in our sample: one that characterizes hyraxes, mole-rats, and carnivores, and another that characterizes hares and bovids. Faunal analysts investigating the potential role of VE at fossil sites should be aware of 1) these taphonomic patterns and differences and 2) that there is no singular pattern of accumulation. We define patterns of preservation, breakage, and bone modification that can be employed on a taxon-specific basis to distinguish VE prey remains from other bone accumulators.

1. Introduction

Over the last 30 years, taphonomy has played a central role in our improved understanding of the natural and cultural processes involved in the formation of fossil assemblages. To this end, actualistic and experimental studies have been instrumental in developing the criteria used to characterize the signatures of several bone accumulating agents (Binford, 1981; Bonnichsen and Sorg, 1989; Brain, 1981; Domínguez-Rodrigo and Piqueras, 2003; Domínguez-Rodrigo et al., 2013; Elkin and Mondini, 2001; Hudson, 1993; Landt, 2007; Marean et al., 1992; McGraw et al., 2006; Munro and Bar-Oz, 2005; Pickering et al., 2005; Pickering and Wallis, 1997; Pobiner et al., 2007; Sanders et al., 2003; Thompson and Henshilwood, 2014). The bulk of this research has focused on carnivorous mammals and humans, and though raptors have been recognized as accumulators of fossil bone (Andrews, 1990; Berger and Clarke, 1995; Fernández-Jalvo et al., 1998; Gilbert et al., 2009; Klein and Cruz-Uribe, 2000; Lloveras et al., 2011; Sampson, 2000), the criteria used to characterize the signatures of their involvement and the range of variability within those signatures remain less-well defined.

This variability is especially true of diurnal raptors such as eagles. Some eagle predation studies (Bochenski et al., 2009; Erlandson et al., 2007; Hockett, 1995, 1996; McGraw et al., 2006; Sanders et al., 2003; Schmitt, 1995; Trapani et al., 2006) have documented fairly minimal levels of damage to eagle prey remains, while other studies (Andrews, 1990; Bochenski et al., 1997; Brain,

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1981; Cruz-Uribe and Klein, 1998; Hoffman, 1988; Lloveras et al., 2008a; Msuya, 1993) have noted considerable bone modification and patterning. This suggests that different eagle taxa capture, consume, and transport their prey in distinctive ways, perhaps depending on the size and/or predator-avoidance behavior of the prey as well as the hunting adaptations of specific eagle taxa. Thus, it is clear that a uniform signature of predation that encompasses all eagle taxa is unlikely to exist.

The specific goals of this paper are to describe the mammalian prey composition and taphonomic signatures of Verreaux's Eagle (*Aquila verreauxii*). Verreaux's Eagle (VE) is a major accumulator of mammal bone in parts of Africa and its potential contribution to Stone Age fossil sites has been recognized (Brain, 1981; Cruz-Uribe and Klein, 1998). Distinguishing between the bones accumulated by different agents such as diurnal raptors, owls, carnivores, and humans is essential to gaining an understanding of human subsistence activity. Consequently, there is a need to distinguish the signatures of VE agency with as much precision as possible as they often roost in and around rock shelters and caves, locations that attract other bone accumulators, including humans. In addition, VE routinely hunt and scavenge prey that other raptors, humans, and carnivorous mammals also target, such as leporids, large rodents, and small bovids. Because of these factors, precise criteria are needed in order to determine what role VE may have played, if any, in the accumulation of bones at fossil sites. This contribution is part of a wider study aimed at elucidating the roles of avian raptors and anatomically modern humans at Die Kelders Cave 1 and Pinnacle Point site 5-6 (Armstrong, A. in prep.).

2. Verreaux's Eagle general habits

VE is a large (male 3.7 kg, female 4.5 kg; wingspan 2.0–2.8 m; height 80–96 cm) diurnal bird of prey that inhabits rocky hill, gorge, and mountain habitats (Hockey et al., 2005). Their distribution is broad, ranging from the Arabian Peninsula to eastern and southern Africa and is generally restricted to areas where annual rainfall is < 750 mm (Hockey et al., 2005). The highest concentrations of VE are found along the mountains of Ethiopia, the highlands of Chad, Angola, Zimbabwe, and South Africa (SA) (Hockey et al., 2005).

VE hunt aerially or from a perch, utilizing stealth and speed to surprise their prey (Gargett, 1990; Hockey et al., 2005). They have also been observed to scavenge carrion and steal prey from other raptors (Gargett, 1990; Steyn, 1982). VE often hunt in pairs (Steyn, 1982). Jenkins (1984) estimated VE's predation rate at 1 kill/30 h. Gargett (1990) approximates that at Matopos Hills, Zimbabwe, a pair of eagles and their eaglet accounted for ~400 hyraxes in a year. By quantifying the prey remains from 73 nest sites in SA, Boshoff et al. (1991) observed that mammals are the primary target of VE – comprising between 81 and 90% of the diet – followed by birds and reptiles. They generally prey on smaller mammals weighing between 1 and 14 kg with an average weight of ~3.5 kg (Hockey et al., 2005) but have been known to take animals up to 20 kg in weight (Steyn, 1982). In SA, rock hyraxes (*Procavia capensis*) frequently constitute between 40 and 90% of the diet (Boshoff et al., 1991; Davis, 1994). This eagle always builds its nests on steep, inaccessible cliffs, rarely in trees (Hockey et al., 2005; Steyn, 1982).

Other common prey taxa include lagomorphs (*Lepus* spp. and *Pronolagus* spp.), large rodents (*Bathyergus suillus* and *Hystrix africaeaustralis*), small bovids (*Raphicerus* spp., *Oreotragus oreotragus*, and a variety of juvenile antelopes), small carnivores (*Felis sylvestris, Cynictis penicillata*, mongooses, and genets), and primates (galagos Family: Galagidae), *Papio ursinus* and *Chlorocebus* spp. *(monkeys)*) (Boshoff et al., 1991; Davis, 1994; Gargett, 1990; Hockey et al., 2005; Steyn, 1982; Zinner and Peláez, 1999). Of their larger mammalian prey (e.g. *H. africaeaustralis*, *P. ursinus*, and antelopes) juveniles tend to be favored (Davis, 1994; Zinner and Peláez, 1999). VE have been reported to scavenge on the remains of large adult mammals such as baboons, zebra, domestic cattle, sheep and goats, and large antelope, bones of which have been occasionally recovered from nest sites (Boshoff et al., 1991; Gargett, 1990; Steyn, 1982). Boshoff et al. (1991) and Gargett (1990) found that medium-to large-sized birds such as Helmeted Guineafowl (*Numida meleagris* and *Guttera eduardi*), francolins and spurfowl (*Francolinus* and *Pternistis* spp.), and bustards (Family: Otididae) are the most common avian prey of VE in southern Africa. Occasionally reptiles like tortoises (common in some areas), snakes, and lizards (especially *Varanus* spp.) are taken (Hockey et al., 2005).

3. Materials and methods

3.1. Study sample

Our study sample consists of prey remains recovered from the area below five nest sites and adjacent feeding perches located in the Cape Floral Region (Fig. 1). All material was collected in discrete phases per nest site between 1988 and 2000; the sample was selected for study as (1) systematic collection at the nest sites and adjacent feeding perches was regularly conducted, (2) the collection criteria included the gathering of all prey remains (undigested bones, fresh and degraded pellets, tortoise, bird and gastropod shell, feathers and fur), and (3) the collections afforded an ample representative sample that could be prepared and studied within a reasonable time-frame. The deposits below the sites were not screened; however, the fact that many small specimens such as teeth and podial bones were collected offers the assurance that the sample accurately reflects the catchment of bone from the nests. The actual nests were not checked for bones as they were built on steep cliffs and inaccessible. However, as is the habit with many birds of prey (Gargett, 1990; Hockey et al., 2005), old bones are periodically cleaned out from the nest and, since the collections were regularly made, much of the potential bias was likely mitigated. In a current study of VEs in the Western Cape Province, M. Murgatroyd (Animal Demography Unit, University of Cape Town, pers. comm.) has observed that some, but not all, nests she accessed

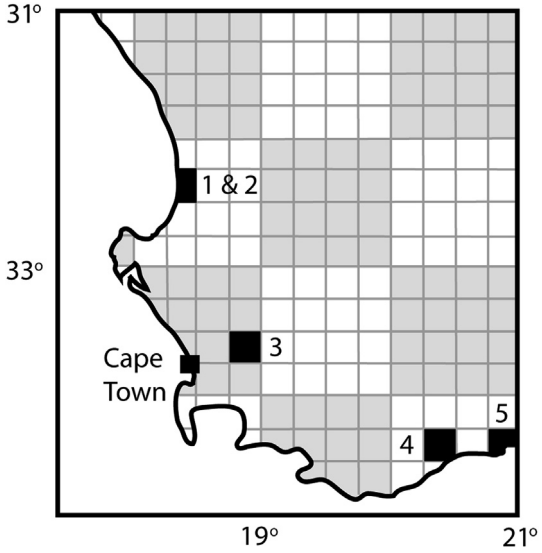

Fig. 1. Location within quarter degree squares of the nest sites from which the Verreaux's Eagle samples were collected: 1-Baboon Point; 2-Verlorenvlei; 3-Agter Paarl; 4-Bloukrans; 5-Windhoek.

had bones on them, but that this would not affect the composition of samples below. In addition to undigested prey remains, a total of five pellets were recovered from the nests and feeding perches.

The specimens required cleaning in order to identify and expose the bone surfaces. Rinsing with cool tap water and agitation with one's fingers was usually sufficient to remove debris. Removal of any remaining tissue was achieved after soaking for four hours in room temperature water. Where implements were required, wooden tools and soft-bristled brushes were used to avoid damage to the specimens. The specimens were not handled again until they were dry. Pellets were broken up by hand and the bones were removed with the aid of forceps. The digested bones were extremely fragile and not rinsed or brushed.

3.2. Taxonomic and skeletal element representation

Skeletal element and taxonomic identifications were made with the aid of the Museum's comparative osteological collection. We recorded the portion of bone preserved and orientation of paired elements. We attempted to identify all specimens, regardless of size, to the highest taxonomic level possible. Taxa cited are from Skinner and Chimimba (2005) and Hockey et al. (2005) for mammals and birds respectively. Most specimens could be identified to a specific skeletal element but a small number of fragmentary specimens lacked diagnostic features and were identified as undifferentiated mammal, bird, reptile, or unidentifiable bone. Most of the undifferentiated specimens are <3 mm in maximum dimension. The vast majority of vertebrate remains were identified to genus and most of these were identifiable to species. However, some bovid specimens could only be identified to size class 1 or 2 of Brain's (1981) bovid size categories. As there were multiple species of hares, bovids, and carnivores identified, these taxa have been grouped in their own respective categories for analytical purposes.

For mammal remains, skeletal element fragmentation was recorded following a method for small mammals described by Lloveras et al. (2008a). This detailed method allows for comparison of skeletal-part frequencies of similar small mammal accumulations and facilitates aggregation of element categories for comparison with other data sets. To estimate skeletal-part frequencies, we calculated the Relative Abundance (RA) of each skeletal element by taxa as defined by Andrews (1990). RA is our preferred method of assessing and comparing skeletal-part frequencies as a number of small mammal assemblages have been reported in this way (Andrews, 1990; Cochard, 2004; Lloveras et al., 2008a, 2008b; 2009; McGraw et al., 2006; Rodríguez-Hidalgo et al., 2013; Sanders et al., 2003; Trapani et al., 2006). We have also calculated percent Minimum Number of Individuals (MNI) and percent Minimum Animal Units (MAU) estimates to facilitate comparisons between other small mammal data sets (Cochard, 2008; Cruz-Uribe and Klein, 1998; Hockett, 1991, 1995; Munro and Bar-Oz, 2005).

3.3. Bone density

To investigate the role of bone structural density in the patterning of prey skeletal-parts we used the closest available bone density values of taxa of similar size and build as density estimates for the prey taxa in our assemblage are not available. For hare and bovid bone density values we substituted *Lepus californicus* (Pavao and Stahl, 1999) and *Ovis aries* (Ioannidou, 2003) respectively. For the mole-rats, hyrax, and small carnivores we used the estimates for *Marmota monax* presented in Lyman et al. (1992). These bone estimates were derived by measuring bone density at specific scan sites on the skeleton using photon densitometry. The bone volume density estimates include both the mineral content and the bone volume measured at the scan site. Though performed on different taxa, the methods and calculations used to derive the bone density values are comparable across the density estimates. Preferably, we would have utilized bone density estimates obtained from computed tomography or photon densitometry that accounts for variation in the shape of bone cross-sections (Lam and Pearson, 2005; Lam et al., 2003). However, we are limited by (1) the number of available comparable datasets, (2) the need to apply density estimates that accurately represent the taxa in our sample, and (3) the methodological necessity of employing density estimates that were obtained with comparable techniques.

3.4. Age and sex

Rock hyraxes (*P. capensis*): We recorded the dental eruption and wear stages of mandibular and maxillary specimens and categorized each based on the rock hyrax eruption and wear schedule devised by Steyn and Hanks (1983). Boshoff et al. and Cruz-Uribe and Klein (1998) established these hyrax eruption states can be employed to group neonates, juveniles, subadults, and adults. We present eruption data on mandibular specimens only as: (1) mandibles are better represented than maxillae and (2) we assume that many of the mandibles and maxillae originate from the same individuals. Hyraxes are sexually dimorphic and can be accurately sexed based on the shape of the upper incisor and incisor alveoli (Thomas, 1892).

Cape dune mole-rats (*B. suillus*): Maxillae with *in situ* cheek teeth can be meaningfully grouped into relative age cohorts (neonate, juvenile, subadult, and adult) based on the dental eruption and wear pattern scheme described by Hart et al. (2007), a methodology similar to those employed by Avery (1990) and Klein and Cruz-Uribe (2000). As with many other rodent species, *B. suillus* is born with some permanent dentition, the P4 and M1, in place (Bennett and Faulkes, 2000). Near the weaning period − 21 days after birth − M2 begins to erupt (Jarvis and Bennett, 1991). The tooth is visible by the time the pup disperses from the nest between 60 and 65 days after birth (Jarvis and Bennett, 1991) and is in full occlusion sometime thereafter. After the pup disperses from the nest and M2 is in or near occlusion, M3 begins to erupt (J.U.M. Jarvis, University of Cape Town, pers. comm.). Based on this schedule and the Hart et al. (2007) tooth-wear and eruption descriptions, we have assigned their tooth-wear and eruption classes to these age cohorts: class 1 = neonates, classes 2–3 = juveniles, classes 4–5 = subadults, and classes 6–9 = adult. At present, a method to accurately sex mole-rat skeletal remains does not exist (though a technique is forthcoming [Montoya-Sanhueza et al., 2013]).

Hares (*Lepus* spp.): As cranial specimens and dentitions are scarcely represented in our hare sample, we follow Hockett (1991, 1995) and Cruz-Uribe and Klein (1998) and present hare postcranial fusion data to provide some information about prey age. Where it can be determined, hares have been divided into adult or juvenile specimens. Sex determination for hares was unattainable.

Bovids (*Family:* Bovidae): We use Hillson's (2005) bovid dental eruption scheme to ascertain age. Hillson depicts and describes four bovid dental eruption categories based on a series of domestic sheep mandibles; because six of our mandibles are *Ovis/Capra* spp. and our sample size is small, we use Hillson's categories to assess all bovids in our assemblage. The age categories are: neonate = deciduous dentition, with deciduous third and fourth premolars erupted and in wear, permanent first molar may be in early stages of eruption; juvenile = mixed dentition, with deciduous third and fourth premolars still present, permanent first molar fully erupted and in wear, and second molar still erupting; subadult = permanent cheek teeth almost complete, with third molar in eruption; adult = full set of permanent cheek teeth, with

the third molar in wear. Few well-preserved bovid cranial specimens were recovered making it difficult to ascertain a sex ratio.

Carnivores: Age assessment criteria for the carnivores in our assemblage do not exist. However, it is possible to provide some information about prey age as several maxillae and mandibles with complete dentitions were preserved as well as long bone epiphyses. Sex ratio determination was not possible given the lack of established methods to determine carnivore sex.

3.5. Surface modifications

All specimens were inspected with a 10–40× binocular zoom microscope under high incident light to examine for and document surface modifications. Bone damage was identified and recorded according to previously-published criteria. Taphonomic indicators such as weathering (Andrews, 1990; Behrensmeyer, 1978), rodent gnawing (Brain, 1981), and post-depositional surface alterations (Thompson, 2005) were recorded but were seldom observed given the collection's modernity and thus lack of exposure. Digestive alteration to teeth and bones was observed and recorded after a system devised by Andrews (1990) and summarized by Lloveras et al. (2008a).

Damage categories were recorded using criteria adopted from established sources in the taphonomic literature; characterization, frequency and location of punctures (Andrews, 1990; Binford, 1981; Blumenschine et al., 1996; Brain, 1981; Elkin and Mondini, 2001; Hockett, 1991, 1995; Landt, 2007; Lyman, 1994; McGraw et al., 2006; Pickering and Wallis, 1997; Pobiner et al., 2007; Sanders et al., 2003; Tappen and Wrangham, 2000; Thompson and Henshilwood, 2014; Trapani et al., 2006), pits (Binford, 1981; Blumenschine and Selvaggio, 1988; Blumenschine et al., 1996; Domínguez-Rodrigo and Piqueras, 2003; Domínguez-Rodrigo et al., 2013; Elkin and Mondini, 2001; Landt, 2007; Pickering and Wallis, 1997; Pobiner et al., 2007; Tappen and Wrangham, 2000; Thompson and Henshilwood, 2014), scores (Binford, 1981; Blumenschine et al., 1996; Bunn, 1981; Elkin and Mondini, 2001; Haynes, 1980, 1982, 1983b; Landt, 2007; Lyman, 1994; McGraw et al., 2006; Pickering and Wallis, 1997; Pobiner et al., 2007; Sanders et al., 2003; Shipman, 1981; Shipman and Rose, 1983; Tappen and Wrangham, 2000; Thompson and Henshilwood, 2014; Trapani et al., 2006), notches (Binford, 1981; Blumenschine and Selvaggio, 1991; Brain, 1981; Capaldo and Blumenschine, 1994; Domínguez-Rodrigo et al., 2013; Fisher, 1995; Haynes, 1982; Landt, 2007; Pickering and Wallis, 1997; Pobiner et al., 2007), crenulated (Binford, 1978, 1981; Brain, 1981; Domínguez-Rodrigo et al., 2013; Elkin and Mondini, 2001; Fisher, 1995; Lyman, 1994; Pickering and Wallis, 1997; Landt, 2007) and fractured edge (Binford, 1981; Domínguez-Rodrigo et al., 2013; Johnson, 1985; Landt, 2007; Pickering and Wallis, 1997) were recorded according to previously-published criteria.

Table 1
The taxa represented in the Verreaux's Eagle nest sites (NISP = number of identified specimens; MNI = minimum number of individuals).

Species	NISP	MNI	% NISP	% MNI
Mammals	**2974**	**371**	**87.1%**	**88.1%**
Procavia capensis (Rock hyrax)	1497	193	43.9%	45.8%
Bathyergus suillus (Cape dune mole-rat)	710	108	20.8%	25.7%
Lagomorphs	595	37	17.4%	8.8%
Lepus capensis (Cape hare)	119	7	3.5%	1.7%
Lepus saxatilis (Scrub hare)	144	13	4.2%	3.1%
Lepus spp. (hares)	332	17	9.7%	4.0%
Bovids	104	14	3.0%	3.3%
Raphicerus spp. (Grysbok/steenbok)	23	5	0.7%	1.2%
Ovis/Capra spp. (Sheep/goat)	16	4	0.5%	1.0%
Bovid size 1	37	3	1.1%	0.7%
Bovid size 2	28	2	0.8%	0.5%
Carnivores	54	14	1.6%	3.3%
Genetta spp. (Genet)	2	1	0.1%	0.2%
Herpestes ichneumon (Large grey mongoose)	1	1	0.0%	0.2%
Galerella pulverulenta (Cape grey mongoose)	51	12	1.5%	2.9%
Micro mammal	14	5	0.4%	1.2%
Otomyinae indet.	4	4	0.1%	1.0%
Micro mammal indet.	10	1	0.3%	0.2%
Birds	**177**	**24**	**5.2%**	**5.7%**
Columba spp. (Pigeons)	91	11	2.7%	2.6%
Raptors	54	3	1.6%	0.7%
Aquila sp. (Large eagle) cf *A. verreauxi*	52	2	1.5%	0.5%
Bubo africanus (Spotted eagle-owl)	2	1	0.1%	0.2%
Swifts and starlings	20	6	0.6%	1.4%
Onychognathus morio. (Red-winged starling)	15	5	0.4%	1.2%
Tachymarptis melba (Alpine swift)	5	1	0.1%	0.2%
Galliformes	12	4	0.4%	1.0%
Franolinus/Pternistis spp. (Francolin/spurfowl)	3	1	0.1%	0.2%
Numida meleagris (Helmeted guineafowl)	9	3	0.3%	0.7%
Tortoise	**257**	**25**	**7.5%**	**5.9%**
Chersina angulata (Angulate tortoise)	257	25	7.5%	5.9%
Fish	**5**	**1**	**0.1%**	**0.2%**
Undifferentiated				
Mammal	37	–	–	–
Bird	26	–	–	–
Tortoise	27	–	–	–
Indet. bone	29	–	–	–
Total NSP	3532	–	–	–
Total NISP	**3413**	**421**	**-**	**99.9**

3.6. Fragmentation

To determine whether the bones were fractured when fresh, the morphology of the fracture angle, fracture outline, and fracture edge were recorded for all long bone shaft fragments following Villa and Mahieu (1991). As comparable small mammal bone breakage data does not exist, we compared our breakage data to the French Neolithic sites studied by Villa and Mahieu. The sites are a suitable comparison as the Fontbrégoua collection was fractured when fresh and Sarrians was broken when dry.

3.7. Specimen and feature measurements

The maximum length and width of each specimen was measured using digital calipers. To estimate bone puncture size, we measured and recorded the length and width at the maximum dimensions and together with the shape of the puncture, size was calculated in millimeters squared. Most punctures were easily categorized into one of four shapes: circular, oval, rectangular, or triangular. Punctures that could not be defined as such were categorized as irregular. Maximum notch breadth was measured parallel to the fracture edge after Capaldo and Blumenschine (1994). All measurements were rounded to the nearest tenth of a millimeter.

3.8. Statistical analysis

We used hierarchical cluster analysis (Neff and Marcus, 1980; Romesburg, 1984) in order to determine which taxa are similar with respect to (1) skeletal-part representation and (2) bone fragmentation. For each of these two variables the values of the resemblance coefficients are arranged in dendrograms representing the hierarchy of similarities among the taxa. In addition, we use principal components analysis to verify the strength of the cluster analyses (Podani, 1994) and report the total variance attributable to each cluster. Binomial logistic regression analysis (Hosmer et al., 2013) was used with respect to (1) bone fragmentation and (2) bone surface modification due to their dichotomous nature (i.e. two possible values, modified or not). This multivariate procedure

permits the discovery of complex relationships between one or more dependent categorical variables (fragmentation and surface modification) and a set of nominally scaled independent variables (taxa and skeletal elements) and is used to identify independent variables that are significantly associated with the dependent variable. All statistical analyses were performed with the software program R, version 2.15.3.

4. Results

4.1. Prey composition

We identified 3532 (n) specimens from the VE nests, of which 3413 (NISP) were identifiable to skeletal element and taxon (Table 1). The specimens represent no fewer than 421 (MNI) individuals from at least 19 different taxa. Of the 421 individuals identified, 371 (88.1%) were mammals, 25 (5.9%) were tortoises, 24 (5.7%) were birds, and one (0.1%) was a fish. Based on MNI the most common prey taxa are rock hyraxes (45.8%), Cape dune mole-rats (25.7%), hares (8.8%), tortoises (5.9%), bovids (3.3%), small carnivores (3.3%), pigeons (2.6%), followed by swifts and starlings (1.4%). Included in these counts are 14 (NISP) specimens retrieved from five pellets.

A small portion of the assemblage could not be identified to a specific taxon or skeletal element: 37 n (1.0%) are undifferentiated mammal, 26 n (0.7%) are undifferentiated bird, 27 n (0.7%) are undifferentiated tortoise, and 29 n (0.8%) are undifferentiated indeterminate bone. All undifferentiated bone was excluded from further analysis since such material is likely to derive from identified individuals.

4.1.1. Mammals

Mammals represent the largest prey class recovered from the VE nest sites, accounting for 2974 NISP (87%). Over 97% of the mammal bones were identified to at least the level of genus and all are terrestrial species. The remains of at least 10 different mammalian taxa were identified, comprising an MNI of 371. Small mammals (those weighing between 500 g and 4.5 kg adult body weight) dominate the assemblage with 2856 NISP (84%) and 352 MNI (84%). Bovid size classes 1 and 2 are represented by 60 NISP (1.8%) and 8 MNI (1.9%), and 44 NISP (1.3%) and 6 MNI (1.4%) respectively. Micromammals (<500 g adult body weight) are represented by 14 NISP (0.4%) and 5 MNI (1.2%).

Rock hyraxes: Hyraxes are the most abundant prey in the VE sample with 1479 NISP (43.9%) and 193 MNI (45.8%). Of the specimens that could be sexed, 46 (45.1%) were females and 56 (54.9%) were males. Of the mandibles that could be aged, 9 (5%) are neonates, 35 (18%) juveniles, 48 (25%) sub-adults and 101 (52%) adults.

Cape dune mole-rats: Mole-rat remains account for 710 NISP (20.8%) and 108 MNI (25.7%) in our assemblage. Of the maxillae that could be aged, adults are the dominant cohort in the assemblage: 0 neonates, 2 juvenile, 6 sub-adult, and 45 adult.

Hares: We identified Cape hare (*Lepus capensis*) and scrub hare (*L. saxatilis*) but did not find Smith's red rock rabbit (*Pronolagus rupestris*) in our prey assemblage. Hares account for 595 NISP (17.4%) and 37 MNI (8.8%) of the assemblage. Hare remains are dominated by adult individuals as the vast majority of humeri (85.7%) and tibiae (80.4%) are fused at both the proximal and distal ends.

Bovids: Bovid skeletal remains are represented in the assemblage by 104 NISP (3.0%) and 14 MNI (3.3%). We identified *Raphicerus* spp. and *Ovis/Capra* spp. as well as specimens that could only be identified to either bovid size class 1 or 2. We found only one adult mandible (8%); all others were classified as sub-adults or younger (92%). Juveniles are the most abundant age-class, accounting for 62% of the aged mandibles.

Carnivores: At least three small carnivore species are present: *Genetta* spp., *Herpestes ichneumon*, and *Galerella pulverulenta*. As a group they account for 54 NISP (1.6%) and 14 MNI (3.3%). All of the small carnivore cranial specimens exhibit fully-erupted adult dentitions in varying degrees of wear; there are no sub-adult cranial specimens in the sample. In addition, all carnivore long bones are fused at the proximal and distal ends.

4.2. Skeletal-part representation and survivorship

Percent RA, MNI, and MAU are presented in Table 2 and Fig. 2. It should be pointed out that because our MNE values were summed over five separate nest sites, there are no RA values for hares, bovids, or carnivores that reach 100%. Fig. 3 provides a hierarchical cluster diagram of the five prey aggregates arranged by similarities in skeletal-part representation, while Table 3 contains the principal component values for the comparisons between the skeletal-part frequencies of each prey taxa. Our cluster analysis indicates that there are two patterns of skeletal-part preservation among the five mammalian prey aggregates. While bearing in mind differences in sample size, it appears that hyrax, mole-rat and carnivore bones are similarly differentially preserved and differ from the skeletal-part pattern of hares and bovids. Our principal components analysis supports the cluster analysis as PC1 has the largest loadings for hyrax, mole-rat, and carnivore. These taxa are approximately equal and they explain 68.5% of the variation in the data. The second PC explains almost all the remaining variation as PC2 loads for hares and bovids.

The abundance of maxillae and mandibles among the hyraxes, mole-rats, and carnivores is particularly conspicuous in comparison to hares and, to lesser extent, bovids. Another striking pattern is the lack of most postcranial remains among the hyraxes, mole-rats, and carnivores, a notable exception being the relative frequency of preserved hyrax pelves. There is a tendency among all five prey groups for hind limb elements (pelvis, femur, and tibia) to outnumber forelimb bones (scapula, humerus, radius, and ulna) and for upper-limb (humerus and femur) to outnumber lower-limb elements (ulna, radius, and tibia), with different degrees of variation among the prey aggregates (Table 4). With the exception of hares, axial/torso bones (vertebrae, sacrum, and ribs) are minimally represented among the prey groups. Autopodial elements are scarce for all taxa.

Of the five prey aggregates only hares ($p = 0.01$; $r_s = 0.5217$) have a significant, positive relationship between bone survivorship and bone structural density (Fig. 4). For hyraxes ($p = -0.23$; $r_s = 0.273$), carnivores ($p = -0.21$; $r_s = 0.323$), mole-rats ($p = -0.06$; $r_s = 0.782$), and bovids ($p = -0.19$; $r_s = 0.455$) there is a weak, negative correlation between bone survivorship and density. None of these results are statistically significant, however. Conversely, four of the five prey aggregates exhibit positive and significant relationships between mean maximum dimension and bone survivorship (Fig. 5). Hares ($p = 0.003$, $r_s = 0.614$), hyraxes ($p \leq 0.001$, $r_s = 0.704$), mole-rats ($p \leq 0.001$, $r_s = 0.815$), and bovids ($p = 0.007$, $r_s = 0.616$) all exhibit positive and significant relationships between these attributes; only carnivores show a weak, negative correlation ($p = 0.387$, $r_s = 0.308$).

4.3. Bone fragmentation and breakage

Our sample is dominated by long bones with oblique, v-shaped, and smooth breaks (Table 5). This breakage pattern typifies 'green' fracturing (Haynes, 1983a; Johnson, 1985; Villa and Mahieu, 1991). Nearly half of all mammal bones (45.9%) in the VE sample are

Table 2
Minimum number of elements (MNE), percent relative abundance (%RA), percent minimum number of individuals (%MNI), and percent minimum animal unit (%MAU) values for the mammals recovered from the Verreaux's Eagle nests.

Skeletal element	Hyrax				Mole-rat				Hare				Bovid				Carnivore			
	MNE	%RA	%MNI	%MAU	MNE	%RA	%MNI	%MAU	MNE	%RA	%MNI	%MAU	MNE	%RA	%MNI	%MAU	MNE	%RA	%MNI	%MAU
Crania (Maxilla)	352	91%	93%	94%	209	97%	100%	100%	11	15%	16%	19%	3	11%	33%	23%	22	79%	100%	100%
Mandible	373	97%	100%	100%	111	51%	56%	53%	2	3%	5%	3%	13	46%	100%	100%	10	36%	50%	45%
Incisors (iso.)	54	5%	6%	0%	5	1%	4%	0%	9	6%	14%	0%	0	0%	0%	0%	0	0%	0%	0%
Up ck. teeth (iso.)	12	0%	1%	0%	16	2%	5%	0%	0	0%	0%	0%	0	0%	0%	0%	2	3%	8%	0%
Low ck. teeth (iso.)	12	1%	1%	0%	9	1%	5%	0%	0	0%	0%	0%	0	0%	0%	0%	0	0%	0%	0%
TEETH TOTAL	78	1%	6%	1%	30	1%	13%	1%	9	1%	14%	1%	0	0%	0%	0%	2	1%	8%	0%
Atlas	4	2%	2%	2%	0	0%	0%	0%	0	0%	0%	0%	1	7%	11%	15%	0	0%	0%	0%
Axis	1	1%	1%	1%	0	0%	0%	0%	0	0%	0%	0%	0	0%	0%	0%	0	0%	0%	0%
Cervicals	10	1%	1%	1%	3	0%	1%	1%	2	1%	3%	1%	1	1%	11%	3%	0	0%	0%	0%
Thoracics	24	1%	2%	1%	2	0%	1%	0%	13	3%	5%	4%	0	0%	0%	0%	0	0%	0%	0%
Lumbars	35	3%	3%	2%	9	0%	3%	1%	85	33%	38%	41%	0	0%	0%	0%	0	0%	0%	0%
Caudal	9	1%	1%	0%	2	0%	1%	0%	0	0%	0%	0%	0	0%	0%	0%	0	0%	0%	0%
Sacrum	4	2%	2%	2%	3	0%	3%	3%	20	54%	54%	68%	0	0%	0%	0%	0	0%	0%	0%
Ribs	12	0%	1%	0%	4	0%	1%	0%	8	1%	5%	1%	2	1%	11%	1%	0	0%	0%	0%
Scapula	27	7%	8%	7%	3	1%	2%	1%	1	1%	3%	2%	1	4%	11%	8%	0	0%	0%	0%
Humerus	26	7%	8%	7%	20	12%	11%	10%	10	14%	22%	17%	8	18%	44%	38%	4	14%	25%	18%
Radius	7	2%	2%	2%	3	1%	3%	1%	12	16%	22%	20%	2	7%	11%	15%	1	4%	8%	5%
Ulna	3	1%	1%	1%	17	8%	10%	8%	9	12%	16%	15%	3	300%	22%	15%	2	7%	17%	9%
Metacarpal	3	0%	1%	0%	0	0%	0%	0%	0	0%	0%	0%	5	14%	33%	31%	0	0%	0%	0%
Pelvis	163	42%	46%	44%	34	16%	22%	11%	59	80%	100%	100%	5	18%	56%	38%	2	7%	8%	9%
Femur	32	8%	11%	9%	26	15%	13%	12%	26	35%	41%	44%	8	29%	44%	62%	3	11%	17%	14%
Patella	4	1%	1%	1%	1	0%	1%	0%	1	1%	3%	2%	1	4%	11%	8%	0	0%	0%	0%
Tibia	16	4%	6%	4%	37	17%	21%	18%	53	71%	89%	90%	8	29%	67%	62%	3	11%	17%	14%
Fibula	6	2%	2%	2%	–	–	–	–	–	–	–	–	2	7%	22%	15%	1	4%	8%	5%
Calcaneus	7	2%	3%	2%	6	3%	5%	3%	16	22%	32%	27%	2	7%	22%	15%	2	7%	8%	9%
Astragalus	10	3%	4%	3%	3	1%	2%	1%	15	20%	30%	25%	2	7%	22%	15%	0	0%	0%	0%
Carpals/tarsals	0	0%	0%	0%	0	0%	0%	0%	2	3%	5%	0%	1	0%	11%	8%	0	0%	0%	0%
Metatarsals	14	2%	2%	1%	8	1%	3%	1%	46	16%	22%	19%	3	11%	22%	23%	0	0%	0%	0%
Phalanx 1/2	22	0%	1%	0%	3	0%	2%	0%	54	4%	24%	5%	5	2%	22%	5%	0	0%	0%	0%
Phalanx 3	1	0%	1%	0%	9	0%	4%	0%	27	4%	24%	5%	0	0%	0%	0%	0	0%	0%	0%

broken (Table 6 and Fig. 6) resulting in a fragmentation ratio of 1.23 (NISP: MNE). Predictably, small compact bones such as tarsals, patellae, and phalanges are among the most intact elements while more delicate bones such as ribs, scapulae, and crania are the least intact across all prey aggregates. Beyond these general observations, it is difficult to summarize across the assemblage as the degree of fragmentation varies by taxon and skeletal element.

To test for fragmentation differences we employed binomial logistic regression analysis, providing tests for differences between taxa adjusting for skeletal elements, and for skeletal elements adjusting for taxa (that is, Type II tests). The results indicate that the fragmentation differences between taxa ($Df = 4$, $p = 0.03$) and between skeletal elements ($Df = 24$, $p \leq 0.01$) are significant at the 0.05 level (Table 7). To further investigate fragmentation similarities and differences between taxa, we used hierarchical cluster analysis to compare fragmented to whole bones by skeletal element. The results indicate that there are three patterns of whole bone preservation among the prey groups (Fig. 7). Mole-rats and carnivores constitute one cluster and hyraxes compose a second, closely-related cluster exhibiting comparable proportions of whole bone preservation across skeletal elements. This pattern differs from the whole-bone preservation of hares and bovids which are similar to one another and constitute a third cluster. Our principal components analysis (Table 3) supports the cluster analysis as PC1 has the largest loadings for mole-rats and carnivores and includes the similarly-fragmented hyraxes. These taxa are approximately equal and they explain 77.8% of the variation in the data. The PC2 explains almost all of the remaining variation and loads for hares and bovids.

4.4. Bone surface modifications

The combined total of surface-modified bone for mammals is 36.9% of NISP (Table 8). (See Inline Supplementary Fig. S1 for the frequency of bone surface modifications broken down by skeletal element and taxon.)

Inline Supplementary Fig. S1 can be found online at http://dx.doi.org/10.1016/j.jas.2014.08.024.

4.4.1. Punctures (Fig. 8)

Punctures are the most conspicuous surface modification observed in the assemblage. Most punctures are macroscopic and can be detected with the naked eye. However, some punctures are extremely small – the smallest is 0.9 mm^2 – and could easily have been missed if not for the use of a microscope. Among the prey aggregates, we observed 276 specimens (9.3% of total NISP) with at least one puncture and 128 specimens had multiple punctures; total number of punctures observed is 460. Carnivore bones (14.8% carnivore NISP) are the most punctured, followed by bovids (13.5% bovid NISP), hyraxes (10.4% hyrax NISP), mole-rats (10.0% mole-rat NISP), and hares (4.5% hare NISP). Punctures almost uniformly occur on specimens with thin cortical bone and underlying trabecular bone, such as crania and mandibles and the epiphyses of long bones and vertebrae. Punctures were not observed on the shafts of long bones and only two occurred on compact bones, a tarsal and a patella.

Cranial bones exhibit the greatest number of specimens with at least one puncture, totaling 138 (15.7% crania NISP). These punctures are more or less evenly distributed across the frontal, parietal, occipital, temporal, and orbital bones; few punctures occur on premaxillae and maxillae. Thirty-four mandibles have at least one puncture (5.8% mandible NISP). Most of these appear on the ramus and gonion, while a few are on the coronoid process, mandibular condyle, and mandibular corpus. There are 84 hind limb bones (pelvis, femur, patella, and tibia) that exhibit at least one puncture (14.1% hind limb NISP). Over half– 47 (56.0% hind limb puncture NISP) – of all hind limb punctures occur on the pelvis; of those

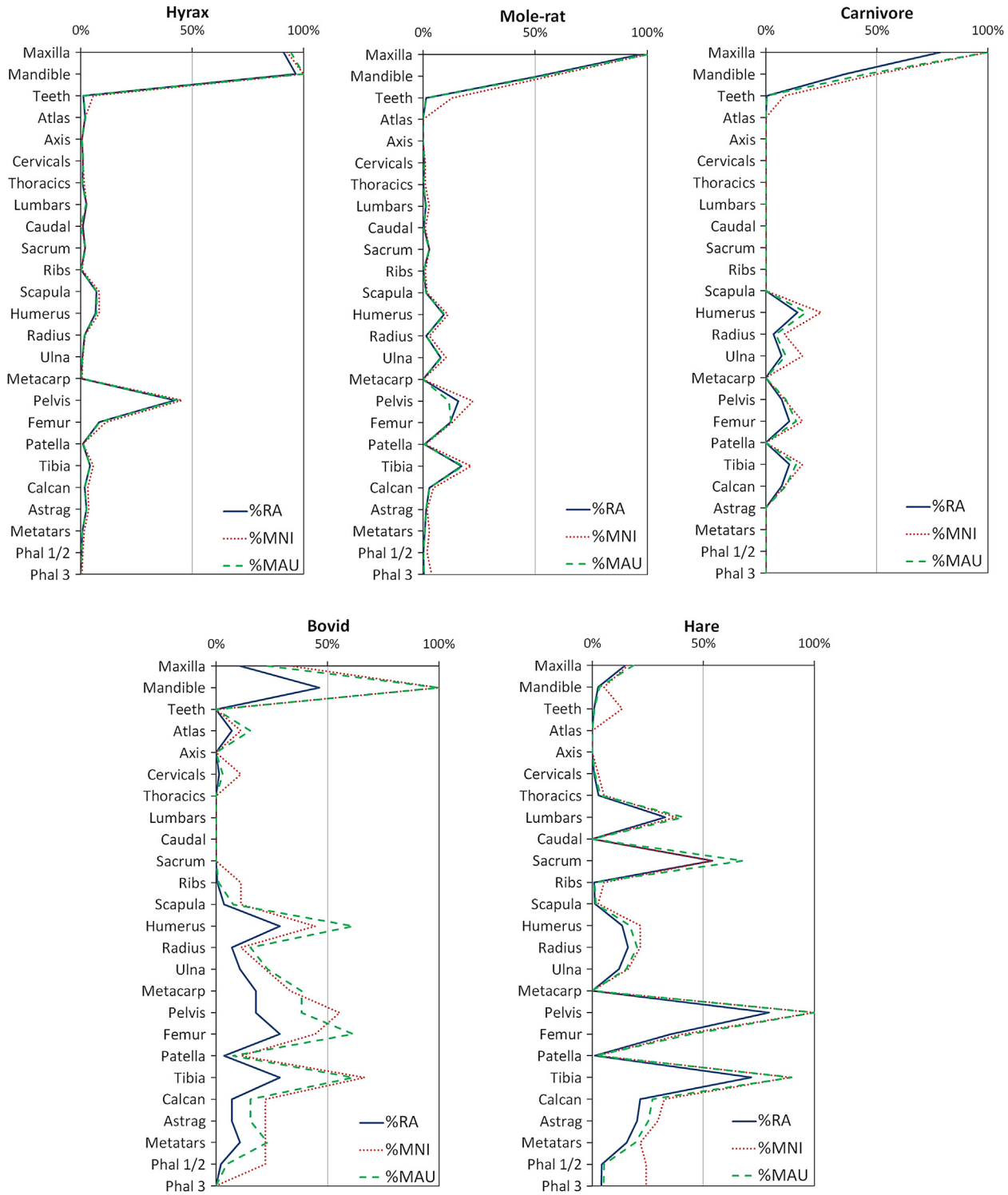

Fig. 2. Skeletal part frequencies (bone survivability) of the mammal prey remains recovered from Verreaux's Eagle nests. Full blue lines = %RA, dotted red lines = %MNI, and dashed green lines = %MAU.

68.5% are located on the ilium. Nineteen femora and 17 tibiae specimens have at least one puncture (12.8% and 10.8% of femora and tibiae NISP). The majority (77.8%) of femoral punctures occur at the distal portion of the bone whereas tibiae punctures mostly (89.5%) occur on the proximal portion. Forelimb (scapula, humerus, radius, and ulna), torso (vertebrae, sacrum, and ribs), and autopodial specimens (carpals, tarsals, metapodia, and phalanges) exhibit the fewest punctures by body part: twelve, four, and four (6.5%, 1.4%, and 1.4% NISP) respectively. Of these elements, only the proximal humerus displays multiple punctures with eight (9.9% humeri NISP).

Table 9 illustrates the shape categories of the observed punctures as well as the location, frequency, minimum, maximum, mean size, and standard deviation of the puncture areas. Oval punctures

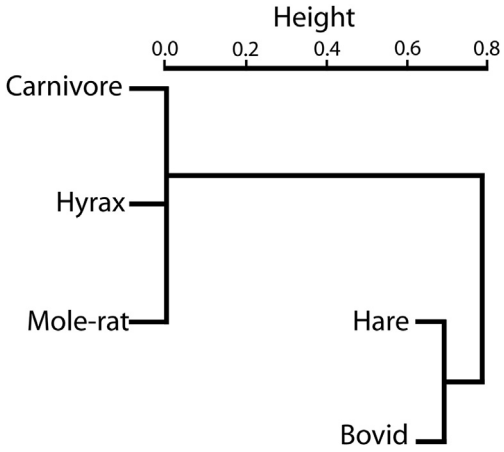

Fig. 3. Cluster dendrogram summarizing the similarities in skeletal-part representation of the mammals recovered from the Verreaux's Eagle nests.

Table 3
Principal component values for comparisons between (1) skeletal-part frequencies and (2) fragmented and whole bones of hyraxes, mole-rats, carnivores, bovids, and hares.

Importance of components:	PC1	PC2	PC3	PC4	PC5
(1) Standard deviation	0.3628	0.2148	0.09731	0.06976	0.01171
(1) Proportion of Variance	0.6847	0.24	0.04925	0.02531	0.00071
(1) Cumulative Proportion	0.6847	0.9247	0.97398	0.99929	1.00000
(2) Standard deviation	1.6293	0.7439	0.4345	0.1066	0.07073
(2) Proportion of Variance	0.7778	0.1621	0.05531	0.00333	0.00147
(2) Cumulative Proportion	0.7778	0.9399	0.9952	0.99853	1.00000

dominate the assemblage with 58.9% of all punctures, followed by circular (16.1%), irregular (13.7%), triangular (7.2%), and rectangular (4.1%). Irregular punctures are the largest on average (18.5 mm^2) followed by rectangular (15.8 mm^2), oval (13.4 mm^2), circular (7.3 mm^2), and triangular (4.8 mm^2). With the exception of irregular punctures, the different puncture types occur in roughly the same proportions across body portions. Irregular punctures disproportionately occur on cranial specimens (88.9% of all irregular punctures) and most of these are found on the thinnest bones of the cranium (orbits and parietals).

4.4.2. Pits (Fig. 9)

We documented 44 specimens (1.5% of total NISP) with at least one pit; nine specimens exhibited multiple pits, totaling 56 pits. Most pits are small and are difficult to locate without the aid of a microscope and angled light. Carnivore bones (3.7% carnivore NISP) are the most pitted, followed by mole-rats (2.7% mole-rat NISP), bovids (1.9% bovid NISP), hyraxes (1.1% hyrax NISP), and hares (0.7% hare NISP). Unlike the pattern observed with punctured specimens, roughly half (23 pits) of the pits we documented occur on dense cortical bone such as long bone shafts.

Hind limb elements exhibit the greatest number, with at least one pit, totaling 22 (3.7% hind limb NISP). Half of these (10 ilium and one ischium) are found on softer portions of the pelvis. However, seven femora and four tibiae (4.7% and 2.5% femur and tibia NISP) exhibit at least one pit on the cortical portions of bones. Cranial and mandibular bones exhibit the second most pits by body part with 20 (1.4% and 1.4% cranial and mandibular NISP). Cranial pits are located mostly on the frontal and parietal bones; mandibular pits are found mostly on the mandibular corpus under the tooth row. Only two (1.1% forelimb NISP) pits were recorded on bones of the forelimb, both on shaft fragments of proximal humeri. There were no pits found on torso or autopodial specimens.

Table 4
Relative numbers of skeletal elements comparing proportions of postcranial to cranial elements (PC/C)[a], lower limb to upper limb elements (ZE/ST)[b], and anterior to posterior limb elements (AN/PO)[c] after Andrews (1990).

Indices	Hyrax	Mole-rat	Carnivore	Bovid	Hare
PC/C	13.6	17.8	21.9	62.5	353.8
ZE/ST	35.3	80.7	64.3	75	131.5
AN/PO	27.3	37.3	68.8	46.9	23.3

[a] Number of femur + humerus/mandibles + maxillae × 100.
[b] Number of tibia + (radius + ulna)/2/femur + humerus × 100. Radius + ulna divided by 2 to correct for number of elements.
[c] Number of scapula + humerus + (radius + ulna)/2/pelvis + femur + tibia × 100. Radius + ulna divided by 2 to correct for number of elements.

4.4.3. Scores (Fig. 10)

There are 41 specimens (1.4% of total NISP) with at least one score. The scores tend to be straight, shallow in depth and U-shaped in cross-section. Most are three to five millimeters in length and do not display a consistent orientation to the bone axis. As with pits, scores are difficult to observe without a microscope. Bovid bones (1.9% bovid NISP) are the most scored, followed by hares (1.8% hare NISP), hyraxes (1.4% hyrax NISP), mole-rats (1.0% mole-rat NISP), and carnivores (0.0% carnivore NISP). There are 27 specimens (66% scored specimens NISP) in which a score and a pit co-occur.

Hind limb elements exhibit the greatest number, with at least one score, totaling 18 (3.0% hind limb NISP). Nine are found on the ilium (3.2% pelves NISP) while two are on the shafts of femora (1.3% femur NISP) and seven are on the tibia shafts (4.4% tibia NISP). Three forelimb elements (1.6% forelimb NISP) have at least one score: one each on the distal scapula, proximal humerus, and distal radius (2.9%, 1.2%, and 3.6% of each NISP). Four bones of the torso (1.4% torso NISP) show at least one score: three lumbar vertebrae (2.3% lumber NISP) and one sacrum (2.7% sacra NISP). Eight cranial and seven mandibular specimens have scores (0.9% and 1.2% crania and mandible NISP). Only one autopodial bone – an astragalus – is scored (0.4% autopodia NISP).

4.4.4. Notches (Fig. 11)

Only two notches were identified in the assemblage (0.1% of total NISP): one is located on the mid-shaft of a bovid femur, the other on the proximal-shaft of a hare tibia. Both are conspicuous and can be observed with the naked eye. Both notches are semi-circular as opposed to arcuate-shaped, and the platform angles are oriented perpendicularly; the maximum notch breadths of the bovid femur and hare tibia are nine and six millimeters respectively.

4.4.5. Crenulated edges (Fig. 12)

A large proportion of the assemblage (261 NISP, 8.8% of total NISP) has crenulated edge damage. The most common area of damage is on the margins of bones, particularly elements that contain thin cortical bone and bone processes, examples include: the spinous and lateral processes of vertebrae, coronoid process of the mandible, and the iliac and ischial bones of the pelvis. Only four long bone specimens – the epiphyses of a humerus, ulna, tibia, and metatarsal – were recorded with crenulated edge damage and there were no small, compact bones that displayed crenulation. This type of damage is macroscopic and can be observed with the naked eye. Carnivore bones (16.7% carnivore NISP) are the most crenulated, followed by hyraxes (11.2% hyrax NISP), mole-rats (7.3% mole-rat NISP), bovids (6.7% bovid NISP), and hares (4.4% hare NISP).

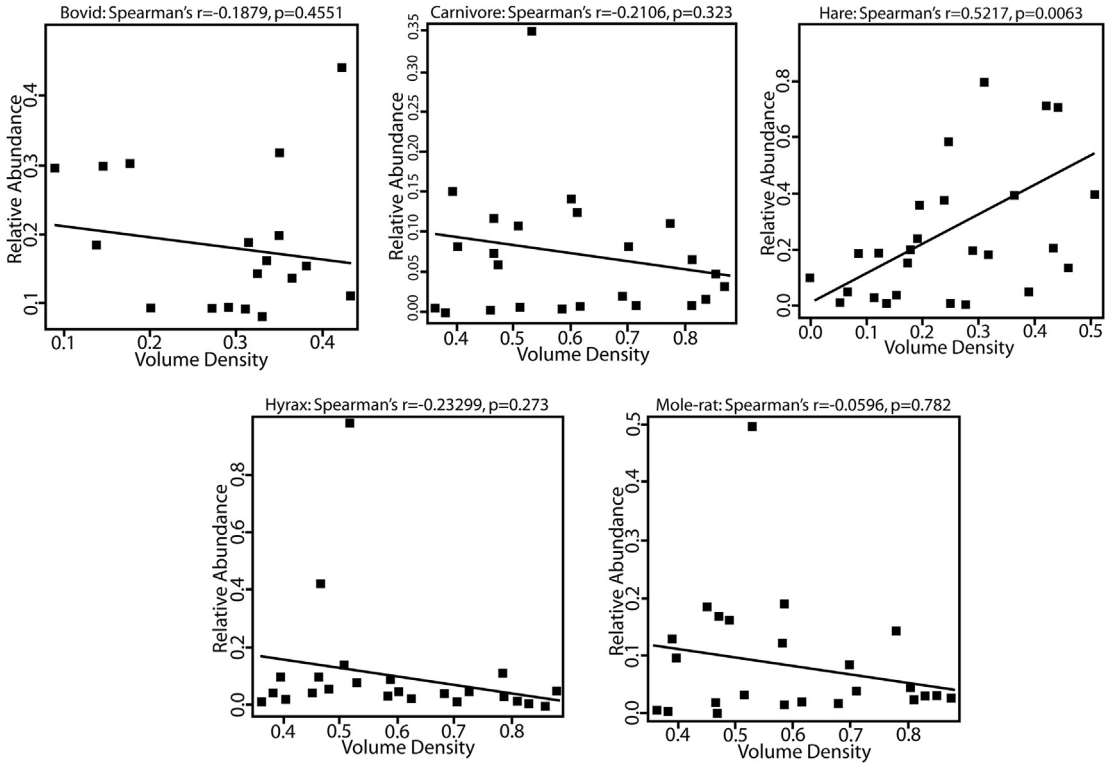

Fig. 4. The relationship between bone density (volume density) and skeletal-element frequency (relative abundance) in the Verreaux's Eagle prey aggregates. Only hares have a positive and significant relationship between the two attributes. Hyraxes, mole-rats, carnivores, and bovids exhibit negative and non-significant relationships between bone density and skeletal-element frequency.

Bones of the torso are the most crenulated (19.9% torso elements NISP): eleven ribs (28.2% rib NISP) exhibit crenulated edge damage, followed by 28 lumbar vertebrae (21.2% lumbar vertebrae NISP), seven sacra (18.9% sacrum NISP), eight thoracic vertebrae (18.2% thoracic vertebrae NISP), and three cervical vertebrae (17.6% cervical vertebrae NISP). Forelimb elements are the second most crenulated (9.7% forelimb elements NISP): 16 scapulae (45.7% scapulae NISP) exhibit crenulated edges, followed by one ulna (2.4% ulnae NISP), and one humerus (1.2% humeri NISP). Cranial and mandibular specimens have 135 examples with crenulation (12.2% mandibles and 7.2% of crania NISP). Fifty hind limb bones (8.4% hind limb elements NISP) are crenulated: 49 pelvis specimens (17.4% pelvis elements NISP) and one tibia (0.6% tibiae NISP). Lastly, one autopodial bone, a proximal metapodial (0.4% autopodial NISP), is crenulated.

4.4.6. *Fractured edges (Fig. 13)*

Fractured edge damage is the most common bone modification in the assemblage, affecting 15.2% of all specimens by NISP. Skeletal elements with dense cortical bone — such as long bones — exhibit fracture damage more frequently than elements comprised of thin cortical and trabecular bone by a ratio of 2.5 to 1. Fractured edge damage was observed throughout the assemblage on a variety of skeletal elements. Bovid bones (32.7% bovid NISP) are the most fractured, followed by hares (16.5% hare NISP), hyraxes (15.4% hyrax NISP), carnivores (14.8% NISP), and mole-rats (11.1% mole-rat NISP).

Seventy one forelimb elements (38.2% forelimb element NISP) have fractured edges: 39 humeri (48.1% humeri NISP), followed by 19 ulnae (45.2% ulnae NISP), nine radii (32.1% radii NISP), and four scapulae (11.4% scapulae NISP). Hind limb elements are the second most fractured (33.8% hind limb elements NISP): 89 femora are fractured (59.7% femora NISP), followed by 80 tibiae (50.6% tibiae NISP), and four metatarsals (44.4% metatarsals NISP). There are 145 fractured cranial and mandibular specimens (9.1% cranial and mandibular specimens NISP). Nineteen torso specimens exhibit fractures (6.6% torso specimens NISP): eight thoracic vertebrae (18.2% thoracic vertebrae NISP), two cervical vertebrae (11.8% cervical vertebrae NISP), and nine lumbar vertebrae (6.8% lumbar vertebrae NISP). Lastly, nine autopodial bones are fractured (3.2% autopodia NISP), all are metatarsals (12.0% metatarsals NISP).

4.4.7. *Digestion (Fig. 14)*

Seventeen identifiable bones and two dental specimens (19 total, 0.6% of total NISP) have digestion damage. Fourteen of these specimens were recovered from the five pellets collected under the nests. In addition to the identifiable specimens, the pellets contained many small but unidentifiable bone fragments. All but seven of these fragments were less than two millimeters in maximum dimension; these seven larger fragments did not have identifiable features and were not assigned to element or taxon. Bovid specimens (1.0% bovid NISP) are the most digested followed by mole-rats (0.8% mole-rat NISP), hyraxes (0.6% hyrax NISP), hares (0.5% hare NISP), and carnivores (0.0% carnivore NISP). While digested specimens could be identified macroscopically, studying them with a microscope aided our ability to assess the extent to which the entire specimen was affected and to observe subtle aspects of digestion — such as rounding and localized pitting. For all digested specimens, the entire bone surface was affected and approximately 50% of the bone was destroyed. Twelve bone and the two dental specimens were graded (Table 1) as "3/heavy" digestion and five bone specimens were graded as "4/extreme" digestion. There were no bones assigned to the lesser two categories "1/light" and "2/moderate."

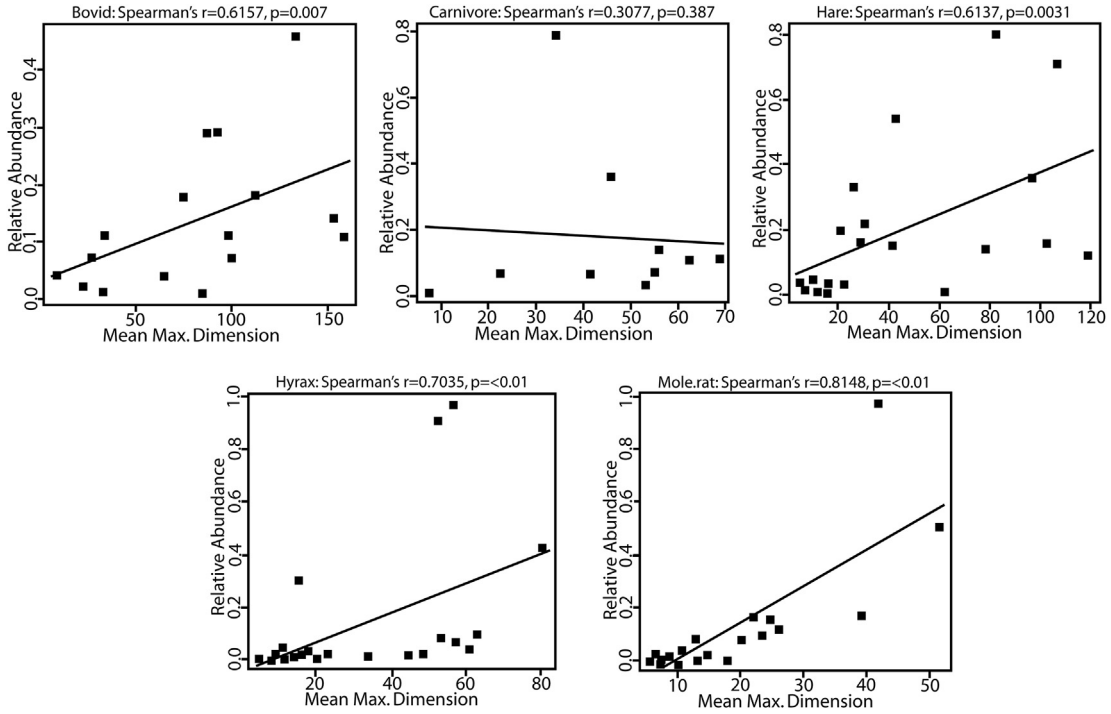

Fig. 5. The relationship between mean maximum dimension of each skeletal element and skeletal-element frequency (relative abundance) of the Verreaux's Eagle prey aggregates. All prey aggregates (except carnivores) exhibit a positive and significant relationship between the two attributes. Only carnivores have a negative and non-significant relationship between mean maximum dimension and skeletal-element frequency. Mean maximum dimension expressed in millimeters.

Table 5
Occurrence of fresh and dry fracture angles, fracture outlines, and fracture edges for long bone shafts of the mammal prey aggregates from the Verreaux's Eagle assemblages.

	Fracture angle (%)			Fracture outline				Fracture edge	
	Oblique (fresh)	Right (dry)	Oblique/right	V-shaped (fresh)	Transverse (dry)	Inter-mediate	Transverse/curved	Smooth (fresh)	Jagged (dry)
Hyrax	59 (75)	11 (14)	8 (10)	56 (72)	9 (11)	1 (1)	12 (16)	67 (86)	11 (14)
Mole-rat	39 (89)	2 (5)	3 (6)	35 (79)	3 (7)	0 (0)	6 (14)	40 (92)	4 (8)
Carnivore	5 (90)	1 (10)	0 (0)	5 (90)	1 (10)	0 (0)	0 (0)	5 (90)	1 (10)
Hare	44 (72)	9 (15)	7 (13)	43 (72)	11 (18)	1 (1)	6 (9)	52 (86)	9 (14)
Bovid	14 (79)	3 (15)	1 (6)	15 (82)	1 (6)	0 (0)	2 (12)	14 (76)	4 (24)

Eight bones of the torso (2.4% torso NISP) with digestion damage, seven vertebrae and one rib. Three forelimb elements (1.6% forelimb NISP) are digested: one distal humerus, a proximal ulna, and a distal radius. Four cranial specimens and two isolated teeth are digested (0.4% crania NISP). There is one digested autopodial specimen (0.4% autopodial NISP), a first phalanx from a juvenile bovid. Two hind limb elements (0.3% hind limb NISP) are digested, a mole-rat pelvis and patella.

4.4.8. Surface modification differences between prey aggregates

There are surface modification frequency differences between the prey aggregates. Fig. 15 shows the relative proportion of surface modifications, where the horizontal bars are proportional to the surface modifications as represented by taxon. Based on Fig. 15 and the previous descriptions, there appears to be little proportional difference between the frequencies of pits, scores, notches, and digestion, whereas punctures, crenulated, and fractured edge specimens exhibit frequency variability between prey aggregates. To test whether these observations are significant, we performed a binomial logistic regression analysis (Table 7), providing tests for differences between taxa adjusted for skeletal elements and skeletal elements adjusted for taxa (Type II tests). In our analyses, the differences between both taxa and skeletal elements were not significant for pits, scores, notches, and digestion. That is, the frequencies and locations of these modifications do not vary in significant ways. Differences at the 0.05 level for both taxa and skeletal elements were observed for punctures ($Df = 4$, $p = 0.02$ and $Df = 42$, $p \leq 0.01$), crenulated ($Df = 4$, $p \leq 0.01$ and $Df = 42$, $p \leq 0.01$), and fractured ($Df = 4$, $p \leq 0.01$ and $Df = 42$, $p \leq 0.01$) specimens. These results indicate that there are significant frequency and location differences for punctured, crenulated, and fractured edge specimens among both taxa and skeletal elements.

5. Discussion

5.1. Prey composition

5.1.1. Rock hyraxes

The fraction of hyrax individuals in our assemblage (45.8% MNI) is less than the MNI reported by Boshoff et al. (1991) acquired from eight VE nests in the Cape Floral Region (60.5% MNI) but is typical of proportions reported in other studies (Hockey et al., 2005). Boshoff et al. (1991) showed that local and regional variation could be influenced by the effects on prey availability of topography. Our age profile is similar to the larger sample (from a range of habitats) of hyrax mandibles from VE nests reported by Cruz-Uribe and Klein

Table 6
Bone fragmentation and specimen size data for the Verreaux's Eagle assemblage: percent whole bone (complete bone/NISP), fragmentation (NISP/MNE), mean, minimum, and maximum size of fragments measured in millimeters.

Skeletal element	Hyrax					Mole-rat					Hare					Bovid					Carnivore				
	%Whole	Fragmen-tation	Mean size	Min. Size	Max. Size	%Whole	Fragmen-tation	Mean size	Min. Size	Max. Size	%Whole	Fragmen-tation	Mean size	Min. Size	Max. Size	%Whole	Fragmen-tation	Mean size	Min. Size	Max. Size	%Whole	Fragmen-tation	Mean size	Min. Size	Max. Size
Crania	48.6	1.41	52.5	9.3	97.8	20.9	1.42	41.9	4.1	81.0	0.0	4.45	41.7	3.8	93.7	0.0	4.67	33.5	10.2	57.4	78.3	1.05	34.2	9.9	64.9
Mandible	44.7	1.10	56.8	8.0	83.5	55.9	1.31	51.7	4.6	76.0	0.0	4.00	15.9	5.4	30.4	43.8	1.23	133.4	46.2	174.6	70.0	1.00	45.9	35.5	50.5
Teeth	70.3	1.17	15.5	4.9	29.3	90.0	1.00	8.6	4.4	46.8	77.8	1.00	9.8	6.7	12.2	–	–	–	–	–	100.0	1.00	7.5	6.7	8.4
Atlas	50.0	1.00	23.4	18.5	26.2	–	–	–	–	–	–	–	–	–	–	100.0	1.00	25.9	25.9	25.9	–	–	–	–	–
Axis	100.0	1.00	17.9	17.9	17.9	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Cervicals	60.0	1.00	11.2	5.5	20.1	100.0	1.00	9.8	6.1	13.7	0.0	1.50	7.5	5.1	9.9	0.0	1.00	32.0	32.0	32.0	–	–	–	–	–
Thoracics	63.0	1.13	11.2	4.2	22.9	50.0	1.00	7.5	7.5	7.6	73.3	1.15	22.5	8.7	32.3	–	–	–	–	–	–	–	–	–	–
Lumbars	54.3	1.00	15.4	4.1	27.9	77.8	1.00	7.2	7.0	75.0	63.6	1.04	26.4	7.1	43.6	–	–	–	–	–	–	–	–	–	–
Caudal	77.8	1.00	9.8	5.5	13.0	100.0	1.00	7.7	6.5	8.8	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Sacrum	50.0	1.00	48.7	27.3	86.5	40.0	1.67	17.7	3.8	31.5	57.1	1.40	42.7	28.4	55.3	–	–	–	–	–	–	–	–	–	–
Ribs	16.7	1.00	10.8	3.3	30.0	7.7	3.25	13.2	8.7	17.7	18.2	1.38	14.6	8.6	24.4	0.0	1.50	84.1	64.0	122.3	–	–	–	–	–
Scapula	66.7	1.00	53.3	20.2	65.6	33.3	2.00	23.6	5.4	41.7	0.0	1.00	62.2	62.2	62.2	0.0	1.00	64.8	64.8	64.8	–	–	–	–	–
Humerus	50.0	1.23	57.6	8.3	78.0	75.0	1.20	26.1	7.8	47.3	81.8	1.10	78.7	20.1	94.9	70.0	1.25	75.3	41.9	99.6	100.0	1.00	56.0	49.1	62.2
Radius	66.7	1.29	44.8	8.1	68.7	50.0	1.33	7.9	3.2	29.5	83.3	1.00	102.8	97.7	109.3	100.0	1.00	100.0	64.3	135.6	100.0	1.00	53.1	53.1	53.1
Ulna	42.9	2.33	34.3	8.1	61.4	70.0	1.18	20.1	15.9	32.3	100.0	1.00	119.3	114.2	125.5	66.7	1.00	98.6	46.5	163.6	33.3	1.50	41.5	15.5	62.4
Metacarpal	100.0	1.00	19.9	17.5	21.5	–	–	–	–	–	–	–	–	–	–	66.7	1.20	154.2	142.5	177.9	–	–	–	–	–
Pelvis	61.8	1.01	80.7	21.8	102.0	77.5	1.18	22.5	9.5	38.3	72.1	1.15	82.8	36.7	103.6	66.7	1.20	111.7	23.5	165.3	100.0	1.00	54.8	44.1	65.4
Femur	35.0	1.88	62.8	9.3	85.0	68.8	1.23	24.5	6.9	40.7	47.7	1.69	97.2	18.2	127.3	70.0	1.25	88.4	25.5	165.4	100.0	1.00	62.4	49.4	68.6
Patella	100.0	1.00	14.4	12.8	16.3	100.0	1.00	7.4	7.4	7.4	100.0	1.00	10.4	10.4	10.4	100.0	1.00	8.6	8.6	8.6	–	–	–	–	–
Tibia	58.3	1.50	60.5	4.4	83.0	71.1	1.25	39.3	8.2	50.6	56.3	1.42	107.2	43.9	144.4	46.7	1.88	91.2	37.3	162.5	66.7	1.00	68.9	53.8	76.5
Calcaneus	100.0	1.00	17.7	16.0	19.4	100.0	1.00	10.5	9.4	11.6	87.5	1.00	30.6	29.6	31.9	100.0	1.00	28.7	27.4	29.9	100.0	1.00	22.5	22.5	22.5
Astragalus	100.0	1.00	11.0	9.5	13.8	100.0	1.00	6.5	5.8	7.2	100.0	1.00	20.8	20.0	21.3	100.0	1.00	27.0	18.5	35.6	–	–	–	–	–
Metatarsals	85.7	1.00	9.1	5.5	11.1	100.0	1.00	14.5	13.3	14.8	86.0	1.09	28.5	9.1	48.5	100.0	1.00	159.6	151.1	180.1	–	–	–	–	–
Phalanx 1/2	67.9	1.27	7.7	4.0	9.9	100.0	1.00	7.3	6.6	7.1	90.7	1.00	9.4	4.0	11.2	100.0	1.00	22.3	18.4	29.1	–	–	–	–	–
Phalanx 3	100.0	1.00	5.2	5.2	5.2	100.0	1.00	6.0	5.6	6.1	100.0	1.00	5.4	2.3	6.1	–	–	–	–	–	–	–	–	–	–
Total/Avg	52.4	1.21	30.1	10.4	43.8	47.7	1.30	17.3	7.2	31.5	64.2	1.24	44.6	25.8	57.1	53.5	1.38	74.4	47.1	101.7	79.2	1.04	44.7	34.0	53.5

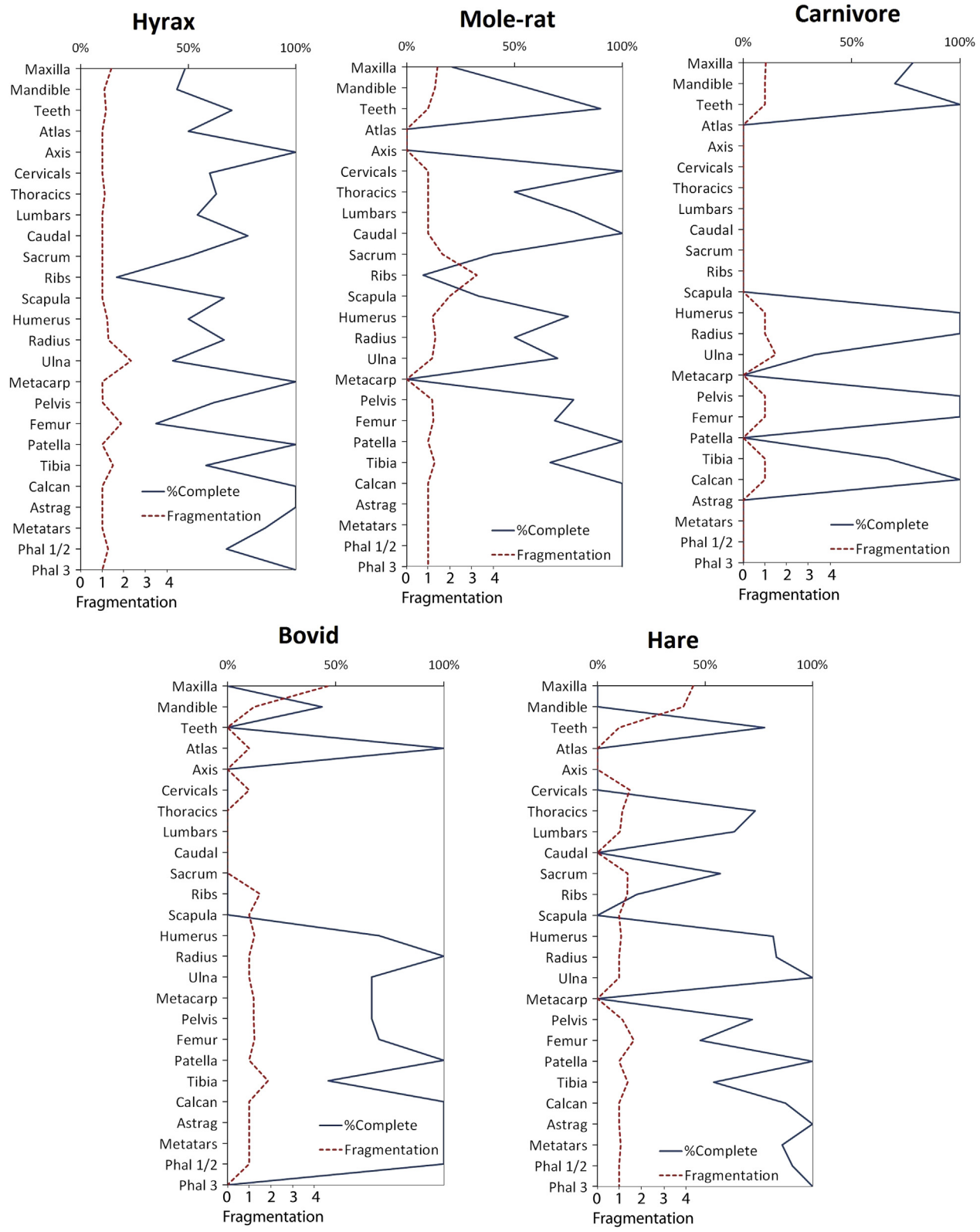

Fig. 6. Completeness of bones (percent whole bones) = blue lines, and bone fragmentation ratio (NISP/MNE) = red lines for the prey aggregates in the Verreaux's Eagle assemblage.

(1998): 207 (7%) neonates, 355 (12%) juveniles, 682 (23%) sub-adults, and 1717 (58%) adults. Cruz-Uribe and Klein observed that neonates are less abundant in the VE assemblages than expected based on their representation in live populations whereas the other age-classes are roughly proportional. They reasoned that, according to Davis (1994), neonates remain closer to rocky shelters to avoid predation as VE are unable to obtain individuals who are situated close to the rock face given their predation strategy of approaching

Table 7
Analysis of deviance (Type II tests): results of binomial regression analyses. Df = degrees of freedom; LR Chi-sq = likelihood ratio chi-square; bold values are significant at the 0.05 level.

Effect	Category	*Df*	LR Chi-sq	*p*
Fragmentation	Taxa	4	10.61	0.03
	Bone	24	765.97	<0.01
Punctures	Taxa	4	12.365	0.02
	Bone	42	256.149	<0.01
Crenulated edges	Taxa	4	40.51	<0.01
	Bone	42	380.34	<0.01
Fractured edge	Taxa	4	49.46	<0.01
	Bone	42	394.66	<0.01
Digestion	Taxa	4	2.461	0.65
	Bone	42	56.073	0.07
Pits	Taxa	4	7.06	0.13
	Bone	42	57.484	0.06
Scores	Taxa	4	3.638	0.46
	Bone	42	59.991	0.35
Notches	Taxa	4	4.336	0.36
	Bone	42	9.785	0.94

at high speed and requiring sufficient space to maneuver. However, seasonal and preservation factors are likely to also contribute to this pattern. Though VE show a preference for hyraxes – accounting for 90% of all prey in some studies (Gargett, 1990) – they do not show preferences for hyraxes of a particular sex or age-class beyond the scarcity of accumulated neonates.

5.1.2. Cape dune mole-rats

Mole-rats are common prey of VE (Hockey et al., 2005). They are represented by a greater fraction in our sample (MNI = 25.7%) than the results Boshoff et al. (1991) reported (MNI = 12.3%). However, as in their results, adults heavily dominate our sample. The adult-dominated age profile is probably not the result of VE prey choice; it is more likely that the underrepresentation of neonates and juveniles reflects the life-history pattern of mole-rats as the neonate and juvenile age cohorts remain cloistered in their natal burrows and are inaccessible to avian predators until adulthood (Bennett and Faulkes, 2000).

5.1.3. Hares

Hares are frequent prey of VE across multiple regions (Boshoff et al., 1991; Gargett, 1990; Hockey et al., 2005) and represent 8.8% (MNI) of our sample. For comparison, leporids were 10.7% (MNI) in the Boshoff et al. (1991) prey assemblage. Adults heavily dominate our assemblage, effectively mirroring the results of Cruz-Uribe and Klein (1998) and approximating Hockett's (1991, 1995) humeri fusion data for leporids accumulated by Golden Eagles (*Aquila chrysaetos*). There are some differences; the VE assemblages exhibit greater frequencies of fused tibia in relation to the Golden Eagle assemblages. The difference may simply be the result of sample size or could reflect differences in predation strategies and/or the ecologies of the hares themselves. Whatever the case, it appears that VE tend to accumulate mature hares. Boshoff et al. reported only 5% juvenile hares in their assemblage. It is possible that VE are deleting young hares from the assemblage by swallowing bones whole and destroying the bones during digestion. But this seems unlikely as the long bones of Cape and especially scrub hare are large and, unlike owls, eagles tend to swallow the bones of their prey less frequently, preferring instead to dismember and swallow boneless portions of their prey (Andrews, 1990; Avery, 1990).

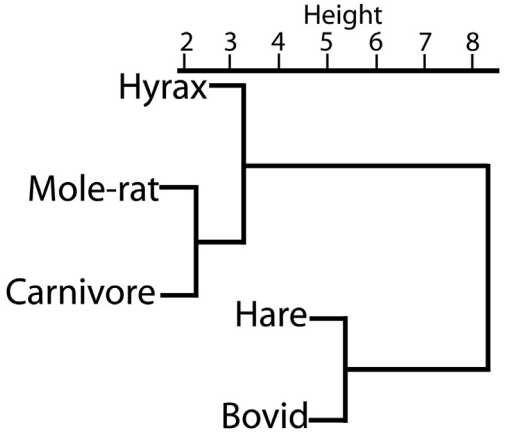

Fig. 7. Cluster dendrogram summarizing the ratio of fragmented to whole bones by skeletal element of the mammals recovered from the Verreaux's Eagle nests.

5.1.4. Bovids

We identified at least two species of bovid and together they represent 3.3% (MNI) of our sample. Boshoff et al. (1991) identified five species and, as a whole, bovids contributed a larger portion of their assemblage, 9.4% (MNI). Boshoff et al. used dental eruption where applicable but only report bovid "juveniles" and "adults." However, the criterion used by Boshoff et al. for aging bovid mandibles was comparable to ours (Avery pers. comm.). The two data sets are similar in revealing that adult bovids are rare in VE assemblages; the number of "adults" reported by Boshoff et al. is 10 individuals (17.5% of bovids).

5.1.5. Carnivores

Boshoff et al. (1991) identified seven species of small carnivores as compared to our three. Carnivores account for 3.3% (MNI) of our sample compared to 6.3% (MNI) in Boshoff et al.'s sample. Like Boshoff et al., we found only adult carnivores in our sample.

The age profiles of prey documented here, and reported elsewhere indicate that VE typically accumulate adult mammals, with the exception of bovids where sub-adult individuals are more common. In this study as well as in others where the sex of the prey has been determined, there does not seem to be a preference for males or females among the taxa. The differences between the proportions of prey represented in our sample and the numbers reported by Boshoff et al. (1991) likely reflect local and sample size differences as their sample consisted of eight nests to our five and included more individuals, an MNI of 608 to our 371. On the whole, the differences are not substantial and we do not think they represent significantly different patterns of predation.

5.2. Skeletal-part representation

The bone relative abundance profiles of VE prey are distinctive. Hyrax, mole-rat, and carnivore prey remains are dominated by cranial and mandibular specimens and, to a lesser extent, hind limb elements. Of notable exception to this pattern is the abundance of hyrax pelves which is the most abundant postcranial element among the prey cluster. However, the abundance of hyrax pelves is minimized by the lack of all other postcrania, squarely placing the hyraxes with mole-rats and carnivores. The hare and bovid profiles noticeably deviate from hyraxes, mole-rats, and carnivores, exhibiting fewer cranial and mandibular specimens and greater frequencies of postcranial elements, particularly axial and fore limb bones. Our cluster and principal components analyses indicate that the differences in the skeletal-parts profile reflect two discrete patterns, one that characterizes hyrax, mole-rat, and carnivore bone survivorship (even when accounting for the relatively high

Table 8
Frequencies and total bone surface modifications by body part of the mammal prey aggregates for the Verreaux's Eagle assemblages.

	(%) Puncture	Pit	Score	Digested	Notch	Cren. Edge	Fract. Edge	Total
Hyrax								
Crania	108 (10.8)	5 (0.5)	10 (1.0)	3 (0.3)	0 (0.0)	79 (7.9)	100 (10.0)	305 (30.6)
Torso	0 (0.0)	0 (0.0)	1 (1.0)	4 (3.9)	0 (0.0)	36 (35.3)	12 (11.8)	53 (52.0)
Forelimb	5 (6.7)	0 (0.0)	0 (0.0)	1 (1.3)	0 (0.0)	15 (20.0)	36 (48.0)	57 (76.0)
Hindlimb	43 (17.0)	12 (4.7)	9 (3.6)	1 (0.4)	0 (0.0)	37 (14.6)	80 (31.6)	182 (71.9)
Autopodia	0 (0.0)	0 (0.0)	1 (1.6)	0 (0.0)	0 (0.0)	0 (0.0)	2 (3.2)	3 (4.8)
Total	156 (10.4)	17 (1.1)	21 (1.4)	9 (0.6)	0 (0.0)	167 (11.2)	230 (15.4)	600 (40.1)
Mole-rat								
Crania	50 (10.6)	13 (2.8)	4 (0.8)	1 (0.2)	0 (0.0)	40 (8.5)	34 (7.2)	142 (30.1)
Torso	1 (2.9)	0 (0.0)	0 (0.0)	2 (5.9)	0 (0.0)	3 (8.8)	0 (0.0)	6 (17.6)
Forelimb	3 (5.6)	2 (3.7)	1 (1.9)	2 (3.7)	0 (0.0)	2 (3.7)	17 (31.5)	27 (50.0)
Hindlimb	16 (13.6)	4 (3.4)	2 (1.7)	1 (0.8)	0 (0.0)	7 (5.9)	28 (23.7)	58 (49.2)
Autopodia	1 (3.4)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	1 (3.4)
Total	71 (10.0)	19 (2.7)	7 (1.0)	6 (0.8)	0 (0.0)	52 (7.3)	79 (11.1)	234 (33.0)
Carnivore								
Crania	6 (17.1)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	8 (22.9)	2 (5.7)	16 (45.7)
Torso	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)
Forelimb	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	3 (37.5)	3 (37.5)
Hindlimb	2 (25.0)	2 (25.0)	0 (0.0)	0 (0.0)	0 (0.0)	1 (12.5)	3 (37.5)	8 (100.0)
Autopodia	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)
Total	8 (14.8)	2 (3.7)	0 (0.0)	0 (0.0)	0 (0.0)	9 (16.7)	8 (14.8)	27 (50.0)
Hare								
Crania	4 (6.1)	1 (1.5)	1 (1.5)	2 (3.0)	0 (0.0)	4 (6.1)	5 (7.6)	17 (25.8)
Torso	3 (2.1)	0 (0.0)	3 (2.1)	1 (0.7)	0 (0.0)	18 (12.4)	7 (4.8)	32 (22.1)
Forelimb	3 (9.1)	0 (0.0)	2 (6.1)	0 (0.0)	0 (0.0)	0 (0.0)	4 (12.1)	9 (27.3)
Hindlimb	16 (8.7)	3 (1.6)	5 (2.7)	0 (0.0)	1 (0.5)	4 (2.2)	75 (40.8)	104 (56.5)
Autopodia	1 (0.6)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	7 (4.3)	8 (4.9)
Total	27 (4.5)	4 (0.7)	11 (1.8)	3 (0.5)	1 (0.2)	26 (4.4)	98 (16.5)	107 (28.6)
Bovid								
Crania	4 (13.3)	1 (3.3)	0 (0.0)	0 (0.0)	0 (0.0)	4 (13.3)	4 (13.3)	13 (43.3)
Torso	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)
Forelimb	1 (6.3)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	1 (6.3)	11 (68.8)	13 (81.3)
Hindlimb	7 (21.9)	1 (3.1)	2 (6.3)	0 (0.0)	1 (3.1)	1 (3.1)	15 (46.9)	27 (84.4)
Autopodia	2 (11.1)	0 (0.0)	0 (0.0)	1 (5.6)	0 (0.0)	1 (5.6)	4 (22.2)	8 (44.4)
Total	14 (13.5)	2 (1.9)	2 (1.9)	1 (1.0)	1 (1.0)	7 (6.7)	34 (32.7)	61 (58.7)
Grand total	276 (9.3)	44 (1.5)	41 (1.4)	19 (0.6)	2 (0.1)	261 (8.8)	449 (15.2)	1092 (36.9)

Crania = crania, mandible, teeth; Torso = vertebrae, ribs, sacrum; Forelimb = scapula, humerus, radius, ulna; Hind limb = pelvis, femur, patella, tibia; Autopodial = carpals, tarsals, metapodials, phalanges.

frequency of hyrax pelves), and another that characterizes hare and bovid bones.

An alternative interpretation is that the skeletal-parts profiles represent three patterns, with hyraxes, mole-rats, and carnivores exhibiting similar skeletal-parts profiles and constituting one cluster, while hares, which might be expected to cluster with the hyraxes, mole-rats, and carnivores due to their similarities in size and body plan, exhibit a different pattern, driven by the near-complete lack of cranial remains. A third pattern, for bovids, is expected as their differences in size and body plan result in different skeletal-parts patterning characterized by a dearth of cranial elements and higher numbers of postcrania.

The dominance of cranial elements among the hyraxes, mole-rats, and carnivores conforms to published accounts of VE feeding behavior (Davis, 1994; Gargett, 1990) and skeletal-parts representation (Brain, 1981; Cruz-Uribe and Klein, 1998) as does the dominance of postcranial remains among the hares (Cruz-Uribe and Klein, 1998). Additionally, the generally low survivorship of postcranial elements for most prey taxa accords with the feeding habits of VE. Gargett (1990) notes that hunting pairs often partially dismember and consume prey before returning to the nest; presumably some prey body parts are left at such expedient consumption sites. Scavenging and caching of body parts is another behavior (Steyn, 1982) that could influence skeletal-part abundance, particularly in larger prey as, owing to their shape and weight, VE may only transport selected portions of a larger carcass to their nest site. This may explain why there are few bovid cranial remains. Contrariwise, the near absence of hare cranial elements cannot reasonably be attributed to size as hyrax cranial elements are similar in size but in great abundance. The absence of hare crania is likely due to the pneumatized character of the lagomorph skull and mandible (Wible, 2007). This lack of robustness probably results in the more thorough deletion of cranial elements during dismemberment and digestion. As for smaller and broken postcranial elements, these are sometimes swallowed whole by eagles, many of which are subsequently digested completely (Avery, 1990; Andrews, 1990; Boshoff et al., 1990; Lloveras et al., 2008a). It is also possible that some small bones and bone fragments were missed in the collection process. Predictably, fragile and smaller elements such as metapodials, carpals, tarsals, phalanges, and vertebrae are less-well represented.

Our analyses of specimen size and bone structural density indicate that in all but one case – carnivores – individual size instead of structural density is positively and significantly correlated with bone survivorship. Only hares exhibit a positive and significant relationship between survivorship and bone density, a result that mirrors the hare bone density and element representation at VE nests reported by Cruz-Uribe and Klein (1998). VE tend to preserve larger bones and delete small ones regardless of bone density. Again, this preservation pattern probably reflects the eagles' feeding and carcass transport behavior where small, compact skeletal elements are swallowed and destroyed during digestion and larger, meaty bones are transported back to the nest where the bones are stripped of flesh and subsequently discarded.

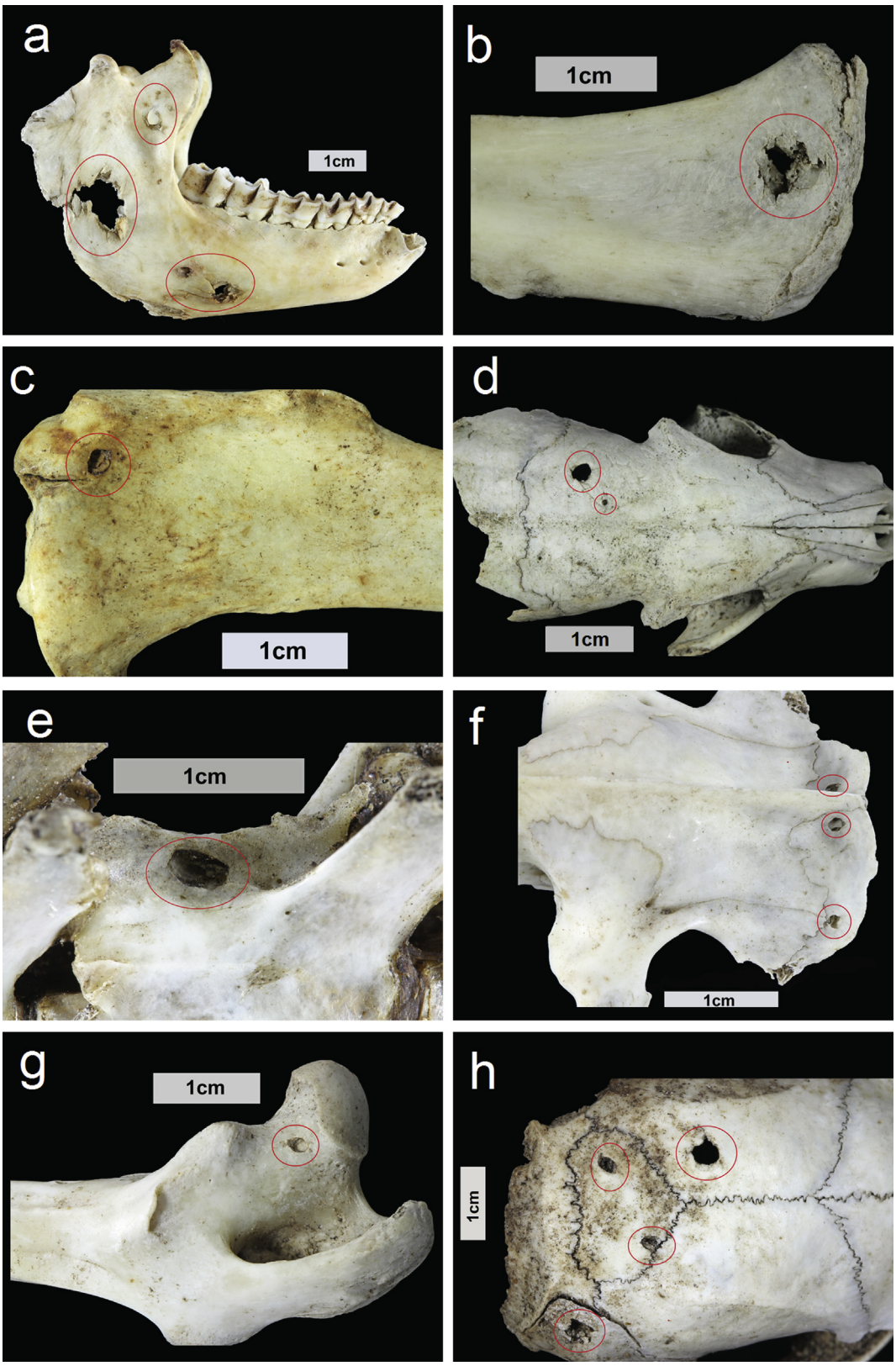

Fig. 8. Puncture damage from the Verreaux's Eagle sample: (8a) *P. capensis* mandible; (8b) *Lepus* spp. ilium; (8c) *Lepus* spp. proximal tibia; (8d) *G. pulverulenta* cranium; (8e) *Lepus* spp. lumbar vertebrae; (8f) *B. suillus* cranium; (8g) *Lepus* spp. proximal femur; (8h) *P. capensis* cranium.

Table 9
Puncture shape categories, location, frequency, minimum, maximum, mean size, and standard deviation for all prey aggregates from the Verreaux's Eagle assemblages.

Puncture type	(%) N	Cranial	Torso	Fore limb	Hind limb	Autopodial	Min. mm^2	Max. mm^2	Mean mm^2	Stand. Dev.
Circular	74 (16.1)	39 (52.7)	0 (0.0)	2 (2.7)	32 (43.2)	1 (1.4)	0.85	62.60	7.25	10.11
Irregular	63 (13.7)	56 (88.9)	0 (0.0)	1 (1.6)	6 (9.5)	0 (0.0)	1.60	58.16	18.48	14.75
Oval	271 (58.9)	202 (74.5)	3 (1.1)	10 (3.7)	55 (20.3)	1 (0.4)	1.11	101.28	13.40	16.53
Rectangular	19 (4.1)	11 (57.9)	0 (0.0	0 (0.0)	7 (36.8)	1 (5.3)	2.58	53.79	15.79	14.24
Triangular	33 (7.2)	19 (57.6)	1 (3.0)	1 (3.0)	11 (33.3)	1 (3.0)	0.86	19.21	4.84	3.96
Total	460	327 (71.0)	4 (0.9)	14 (3.0)	111 (24.1)	4 (0.9)	–	–	–	–

5.3. Bone fragmentation and breakage

There are more broken bones in the VE sample than has typically been reported in other eagle prey assemblages (see Table 10). There are also distinctive patterns of whole bone preservation among the prey aggregates, further suggesting that VE consume individual prey taxa differently. Our logistic regression analysis indicates that fragmentation differences among both taxa and skeletal elements are significantly different. Further, our cluster and principal components analyses demonstrate that mole-rats, carnivores, and hyraxes again exhibit similar proportions of whole bone preservation and that this pattern differs from the whole-bone preservation of hares and bovids which are more analogous to one another.

Our analysis of long bone fractures found that bone fracturing likely occurred during prey capture and consumption rather than through post-discard breakage. The mammal bones from the VE sample closely match the 'green' breakage patterns of the Fontbrégous assemblage, whereas they differ considerably from the Sarrians assemblage, in which breakage took place after the bones had dried.

5.4. Bone surface modifications

Some eagle taxa like the African Crowned Eagle (*Stephanoaetus coronatus*) have been described as "fastidious eaters that inflict little damage to bone" (Sanders et al., 2003). This is clearly not the case for VE. We observed bone surface modifications on roughly one-third of the mammal prey remains. Like bone breakage, surface modifications are more common in the VE sample compared to other eagle prey assemblages (see Table 10). Our detection of bone surface modifications was enhanced by the use of a microscope, notably in relation to small punctures, pits, scores, and digestion. It is possible that where low modification frequencies have been reported the aid of a microscope could result in increased detection of

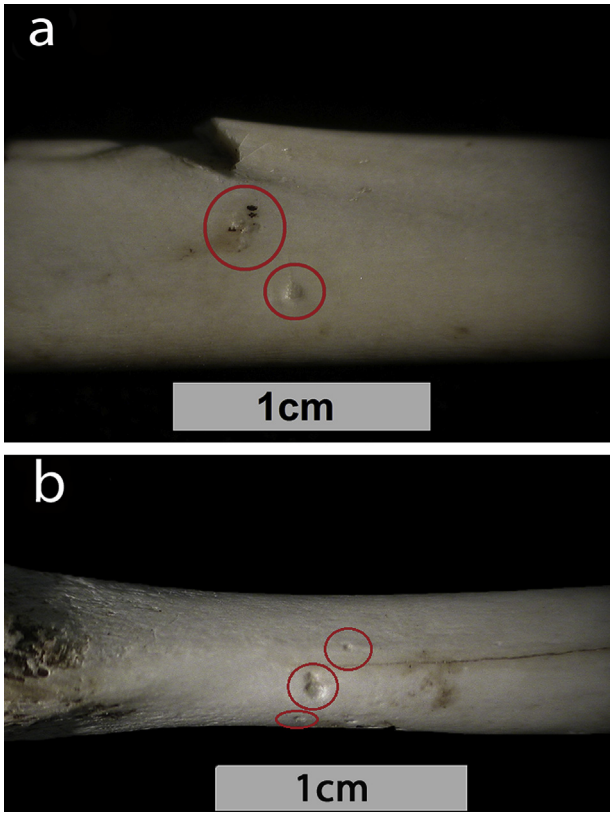

Fig. 9. Pit damage from the Verreaux's Eagle sample: (9a) *B. suillus* tibia mid shaft; (9b) *Lepus* spp. tibia distal shaft.

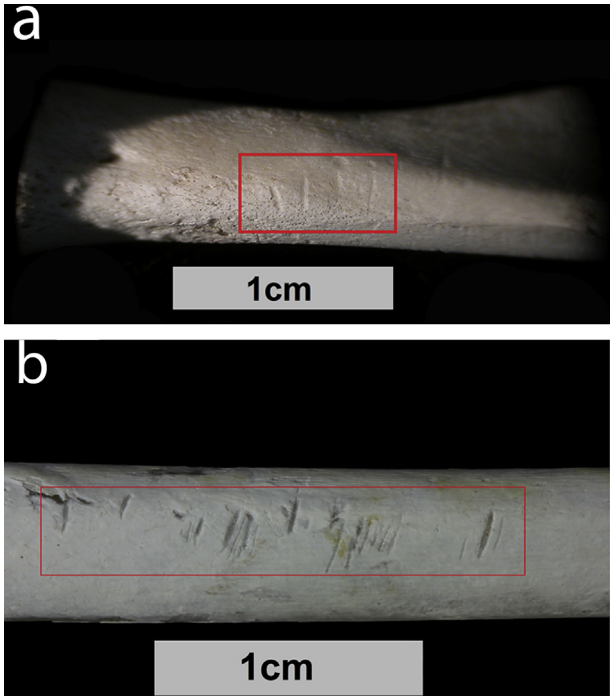

Fig. 10. Scores from the Verreaux's Eagle sample: (10a) *P. capensis* ilium; (10b) *Lepus* spp. radius mid shaft.

Fig. 11. Notch damage from the Verreaux's Eagle sample; two views of the same specimen: (11a) *Lepus* spp. tibia shaft, internal view; (11b) *Lepus* spp. tibia shaft, external view.

bone modifications. However, given the frequency of modifications that are clearly visible with the naked eye, such as large punctures, crenulated and fractured edges (the three most abundant surface modifications), we feel the number of modifications observed reflects the behavior of VE in relation to prey capture and consumption as opposed to the lack of detection in other eagle prey assemblages.

The majority of bone surface modifications appear to have been caused by the beaks or talons of VE during capture and/or consumption. There is no evidence of post-discard ravaging by other organisms, though it is possible that scavengers removed some discarded bones from below the nests and feeding perches. However, Steyn (1982) noted that scavengers tend to avoid foraging below active raptor nests lest they become prey.

Modifications in the form of notches and digested bone were seldom observed. The lack of notches may be due to the fact that VE do not regularly exploit within-bone nutrients as do terrestrial carnivores and humans. The scarcity of digested bone reflects the fact that fewer pellets were recovered than expected, implying that VE swallow few bones and/or tend to regurgitate pellets at places other than nest sites and nearby feeding perches. Moreover, the pellets that were recovered contained many small unidentifiable bone fragments, which indicates that when bones are swallowed they are often destroyed. As has been documented with other species of eagle (Andrews, 1990; Avery, 1990), the aggressive digestion of eagles may simply be deleting many of the bones that are swallowed.

There are significant differences in surface modification between the prey aggregates. Our binomial logistic repression analyses indicate that there are frequency differences for puncture, crenulated, and fractured specimens among the taxa and skeletal elements. There are no differences for pits, scores, notches, and digestion. Fig. 15 shows the relative proportions of modified bone by prey aggregate; it appears that surface modification differences follow a pattern in which hares and bovids display similar proportions of crenulated and fractured specimens and display the two lowest puncture totals by proportion, whereas hyraxes, mole-rats, and carnivores display greater proportions of punctured and crenulated bone but reduced ratios of fractured specimens in relation to hares and bovids. The surface modification patterns offer further confirmation that VE modify and differentially accumulate the bones of their prey in distinctive ways.

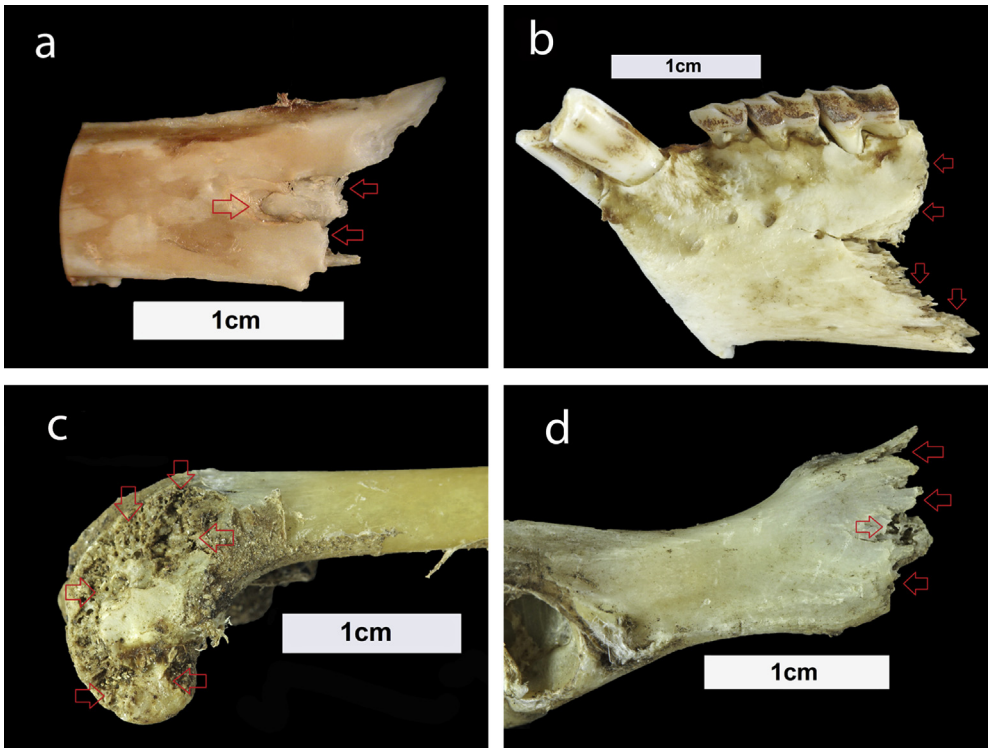

Fig. 12. Crenulated edge damage from the Verreaux's Eagle sample: (12a) *B. suillus* tibia proximal shaft; (12b) *P. capensis* mandible; (12c) *P. capensis* distal femur (12d) *Lepus* spp. ilium.

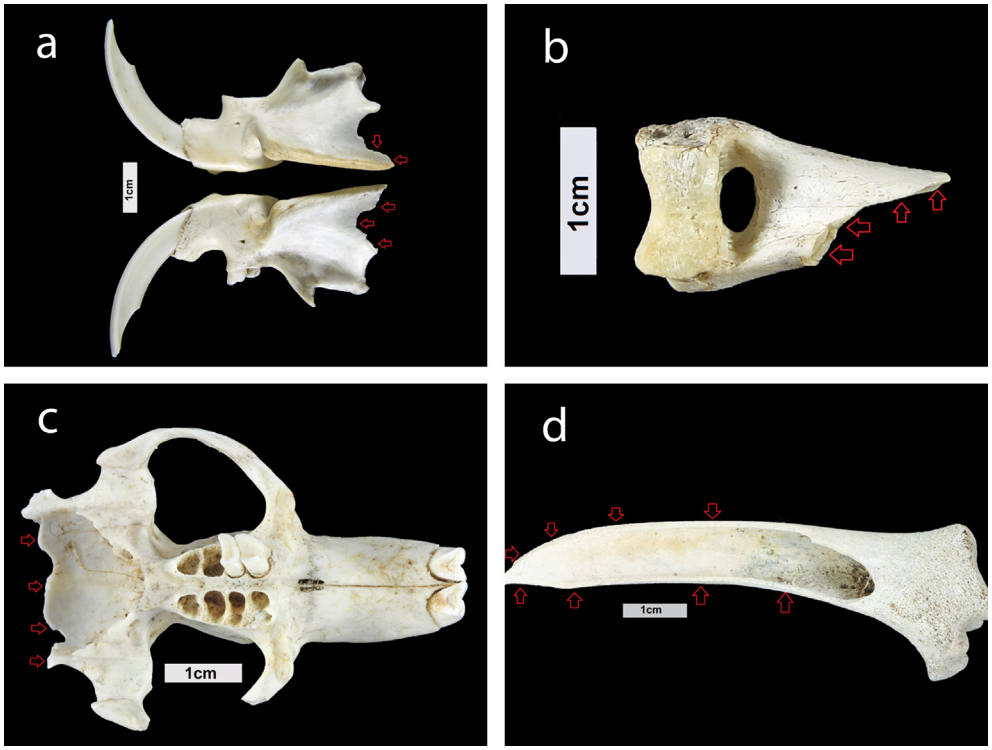

Fig. 13. Fractured edge damage from the Verreaux's Eagle sample: (13a) *B. suillus* paired mandibles; (13b) *P. capensis* distal humerus; (13c) *B. suillus* cranium; (13d) Size I bovid (juvenile) distal femur shaft.

5.5. VE and other small prey accumulators

One of the primary goals of taphonomy is to determine the agents responsible for the accumulation of a fossil assemblage. To achieve this, distinctive bone surface modifications, breakage patterns, and skeletal-part representation of potential accumulating agents must be identified. To date, much work has been done to distinguish the taphonomic signatures of human and carnivore-

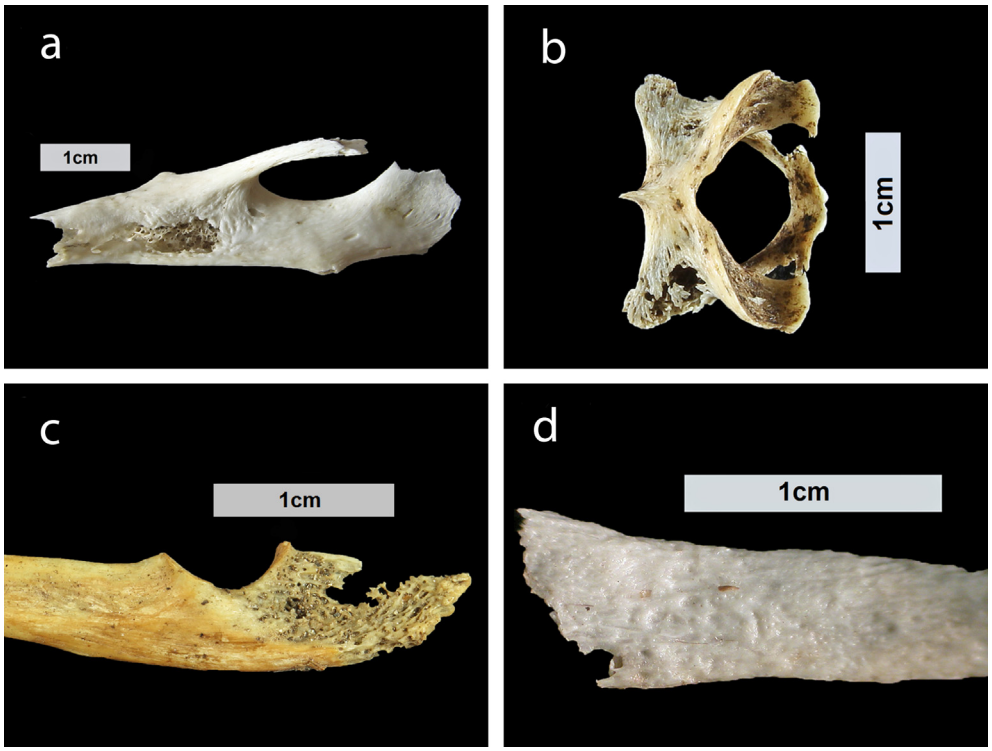

Fig. 14. Digestion damage from the Verreaux's Eagle sample: (14a) *P. capensis* innominate; (14b) *P. capensis* first cervical vertebrae; (14c) *B. suillus* proximal ulna; (14d) *B. suillus* distal radius shaft.

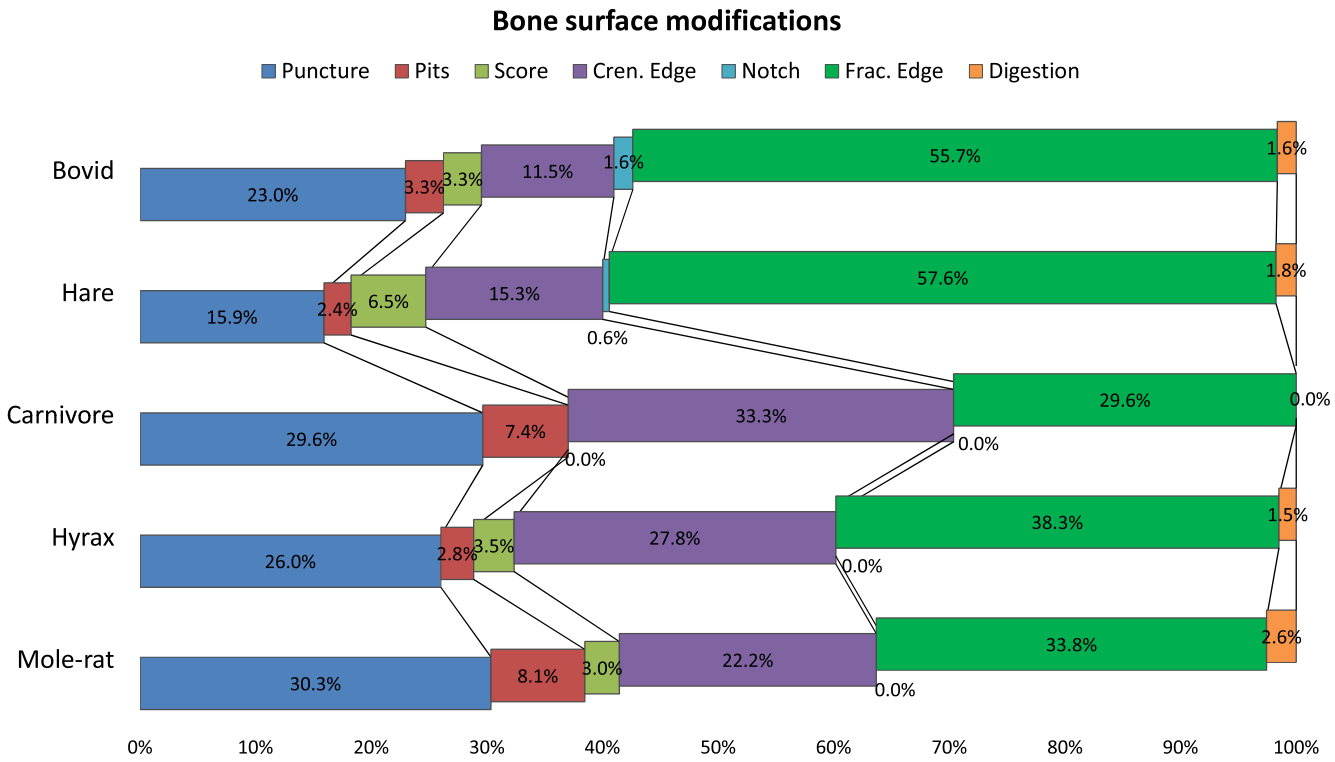

Fig. 15. The relative proportions of bone surface modification in the Verreaux's Eagle samples by prey aggregate. The horizontal bars are proportional to the surface modifications represented by taxon.

accumulated small prey assemblages (Andrews and Evans, 1983; Cochard, 2004, 2008; Hockett, 1999; Hockett and Haws, 2002; Lloveras et al., 2008a, 2011; Lupo and Schmitt, 2002; Mondini, 2004; Munro and Bar-Oz, 2005; Rodríguez-Hidalgo et al., 2013; Schmitt and Juell, 1994; Tagliacozzo and Fiore, 1998; Thompson and Henshilwood, 2014; Yellen, 1991a, 1991b). On the whole, assemblages accumulated by raptors have different taphonomic signatures (Andrews, 1990; Avery, 1990; Bochenski et al., 2009; Hockett, 1991, 1996; Hoffman, 1988; Lloveras et al., 2008b, 2009; Sampson, 2000; Sanders et al., 2003; Trapani et al., 2006) than those accumulated by humans and carnivores. And, among raptors, there are taphonomic differences between diurnal and nocturnal taxa (Andrews, 1990; Avery, 1990; Hockett, 1991, 1996; Lloveras et al., 2008b, 2009), as well as intra-group differences (as documented in this paper).

Table 10 provides small prey skeletal-part preservation, fragmentation, puncture, and digestion comparisons between diurnal and nocturnal raptors and carnivores. In relation to other diurnal raptors, VE contribute conspicuously more damage to the bones of their prey in the form of fragmentation and punctures (usually the only surface modifications, other than digestion, reported in raptor taphonomic studies). They are similar to other diurnal raptors in that cranial and hind limb elements are usually the highest-surviving bones among surface and pellet samples. However, in comparison to nocturnal raptors, VE (and diurnal raptors generally) fragment the bones of their prey far less, resulting in the greater preservation of whole bones. And, though nocturnal raptors tend to swallow and digest prey bones more frequently, VE leave considerably more puncture marks. Skeletal-part preservation patterns between nocturnal raptors and VE (and diurnal raptors generally) are markedly different in that axial, forelimb, and distal-limb elements are better preserved in nocturnal raptor accumulations. Carnivores and VE appear to fragment and puncture the bones of their prey in similar proportions. However, fewer whole bones are preserved in the carnivore assemblages as they often masticate, swallow, and digest the bones of small prey. The patterns of skeletal-part preservation between carnivores and VE are similar in that hind limb elements are usually better represented; they differ in that axial, forelimb, and distal limb elements are better represented in the carnivore assemblages.

6. Conclusions

VE are powerful predators capable of killing and lifting animals beyond their own body weight. They also scavenge from carcasses of prey they could not possibly lift whole. Where their prey accumulations have been quantified, it is apparent that VE are prodigious hunters of small mammals, often specializing on hyraxes. It also appears that there is a correlation between local availability of mammalian prey and prey selectivity by these eagles as the proportion of hyraxes in the diet fluctuates between 40 and 90% and is variously complemented with other locally-available mammals. Based on our study and those of others, hares, mole-rats, bovids, and small carnivores – in addition to hyraxes – comprise the major component of VE diet in the Cape Floral Region. The recovery of multiple skeletal elements from 19 taxa suggests that the variety of prey in our sample adequately represents the range of prey of VE in the Cape Floral region.

Based on the nature and frequency of bone modifications we have observed, it appears that VE inflict more damage to the bones of their mammalian prey than do other eagle species. Broken and punctured specimens are common bone surface modifications observed in our VE sample, whereas these appear to be less common among other eagle prey accumulations. The frequency of damage inflicted by VE indicates that there is taphonomic variability in the ways that different eagle taxa process their prey and,

thereby the accumulations of their prey; there is no "one size fits all" modification pattern for eagles. Taphonomic patterns derived from predation by other eagle taxa do not, therefore, offer the best or appropriate general proxies from which to identify VE predation.

In VE there is patterned variability in the ways they accumulate and modify their prey. There are two distinct skeletal-parts preservation, bone breakage, and bone surface modification patterns among our prey aggregates: one that largely characterizes hyraxes, mole-rats, and carnivores, and another that characterizes hares and bovids. Faunal analysts investigating the potential role of VE at fossil sites should be aware of these taphonomic patterns and differences and that there is no singular pattern of accumulation, especially in regard to skeletal-part preservation. Nevertheless, there are patterns of preservation, breakage, and bone modification that can be employed on a taxon-specific basis to separate VE prey remains from those of other bone accumulators.

Many of the prey taxa found in VE accumulations are common in Stone Age faunal assemblages. Results of this study are contributing to the taphonomic assessment of a Middle Stone archaeological assemblage, which shares many of the taxa described here (Armstrong in prep.).

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Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.jas.2014.08.024.

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